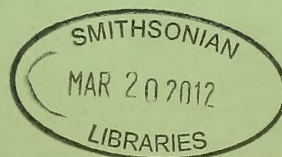
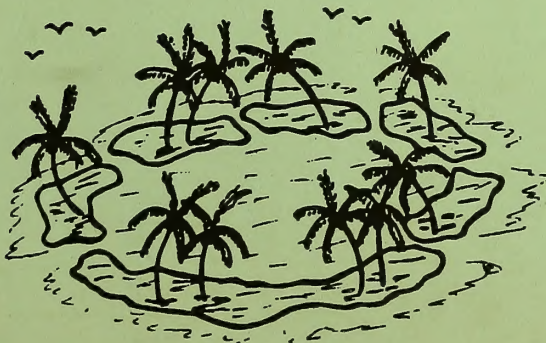


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ATOLL RESEARCH BULLETIN

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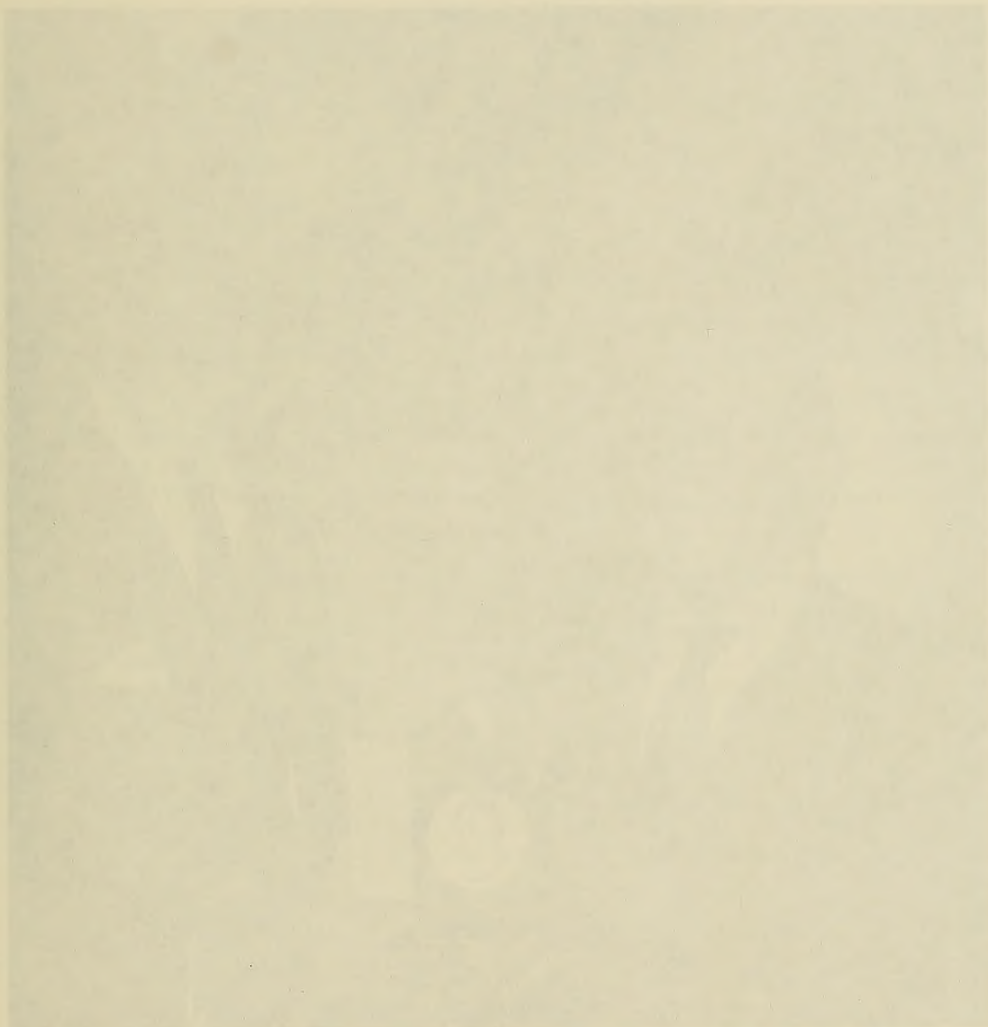
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The following information was obtained from the records of the Department of the Interior, Bureau of Land Management, at Washington, D. C., on July 1, 1941.

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Dr. Coolidge receiving the Edward W. Browning Achievement Award
from S. Dillon Ripley in 1978

Harold Jefferson Coolidge 1904-1985

It saddens us to have to report the death, on February 15, 1985, of Dr. Harold Jefferson Coolidge, whose support as Director of the Pacific Science Board, National Academy of Sciences-National Research Council, was ultimately responsible for the Board's Coral Atoll Program and for the founding and first 15 years of publication of the Atoll Research Bulletin.

Hal was born on January 15, 1904, in Boston, Massachusetts. He received his higher education from Harvard University, and continued his association with Harvard as assistant curator at its Museum of Comparative Zoology from 1929-46. As a professional mammalogist he took part in several expeditions, among them one crossing Central Africa with the Harvard Medical Team in 1926-27, leading the Indo-China Division, Kelley-Roosevelt's Field Museum Expedition 1928-29, and organizing and leading the Harvard Asiatic Primate Expedition, 1937. His work at the Museum resulted in many scientific articles and monographs on the Genus Gorilla, Indo-Chinese Forest Ox or Kouprey, Pygmy Chimpanzee and other primates and mammals.

However, his major reputation was as an enormously successful promoter of research in all fields in the Pacific Basin and especially the islands, and as a leading international conservationist. Together with other scientists interested in the Pacific islands he helped to organize the National Research Council's conference in 1946 that resulted in the establishment of the Pacific Science Board. As the Board's Director from 1946 to 1970 he was responsible for such major research programs as the Coordinated Investigations in Micronesian Anthropology (CIMA), the Scientific Investigations in Micronesia (SIM), and the Coral Atoll Program. He was a major figure in the Pacific Science Association, and served as Secretary General of the Tenth Pacific Science Congress, held in Honolulu in 1961.

In the field of conservation, Hal played a major role in the founding of the International Union for the Conservation of Nature and Natural Resources in 1948, and was principally responsible for bringing the Second Technical Meeting of this new organization to the U.S., at Lake Success, in 1949. He served the Union in many official capacities over the years as Vice President, Chairman of the Survival Service Commission and the International Commission on National Parks, and as President from 1966 to 1972. He was named Honorary President of the Union in 1972.

Hal was the recipient of three Honorary Doctor of Science degrees, and many awards for his international conservation activities, some of which were the J. Paul Getty Wildlife Conservation Prize, the Edward W. Browning Achievement Award, John C. Phillips Medal, and the Gold Medal of the New York Zoological Society.

Our close association with him extended through almost the entire 24 years of the Pacific Science Board. In 1949, in response to a request by the South Pacific Commission for information on coral atoll

ecology, he held a small informal meeting at which the idea of a coral atoll research project was put forward. Coolidge formalized this idea into a proposal to the Office of Naval Research, and it was funded and carried on for over five years during which time major expeditions were sent to five representative atolls in the Pacific. The Atoll Research Bulletin was started in 1951 to make widely available the results of these expeditions and related investigations and studies of coral atolls and reefs. The Coral Atoll Program gave a principal impetus to the enormous amount of work that has been done on coral atolls and reefs since and is still going on under various auspices. This honor is, of course, shared with the U.S. Geological Survey, working on Bikini and other northern Marshall Atolls before and after the atomic bomb tests. Much of our own work was carried out under informal joint sponsorship of the Pacific Science Board and the Geological Survey. The prestige of the Board and its Director drew in grant support that made the non-geological aspects of the atoll and reef research possible. Coolidge's enthusiastic backing for this was unflinching and stimulated the activities of the many participants in the program. Its effects have continued and will be productive under many guises as time and coral reef research go on.

Now, at its end, we salute our friend and his career of many and varied accomplishments. His name will long be remembered, especially in the context of research in the Pacific Ocean area, and of conservation on a global scale.

ATOLL RESEARCH BULLETIN

No. 282

FERAL CATS ON JARVIS ISLAND:
THEIR EFFECTS AND THEIR ERADICATION

BY

MARK J. RAUZZON

ISSUED BY

THE SMITHSONIAN INSTITUTION

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MAY 1985

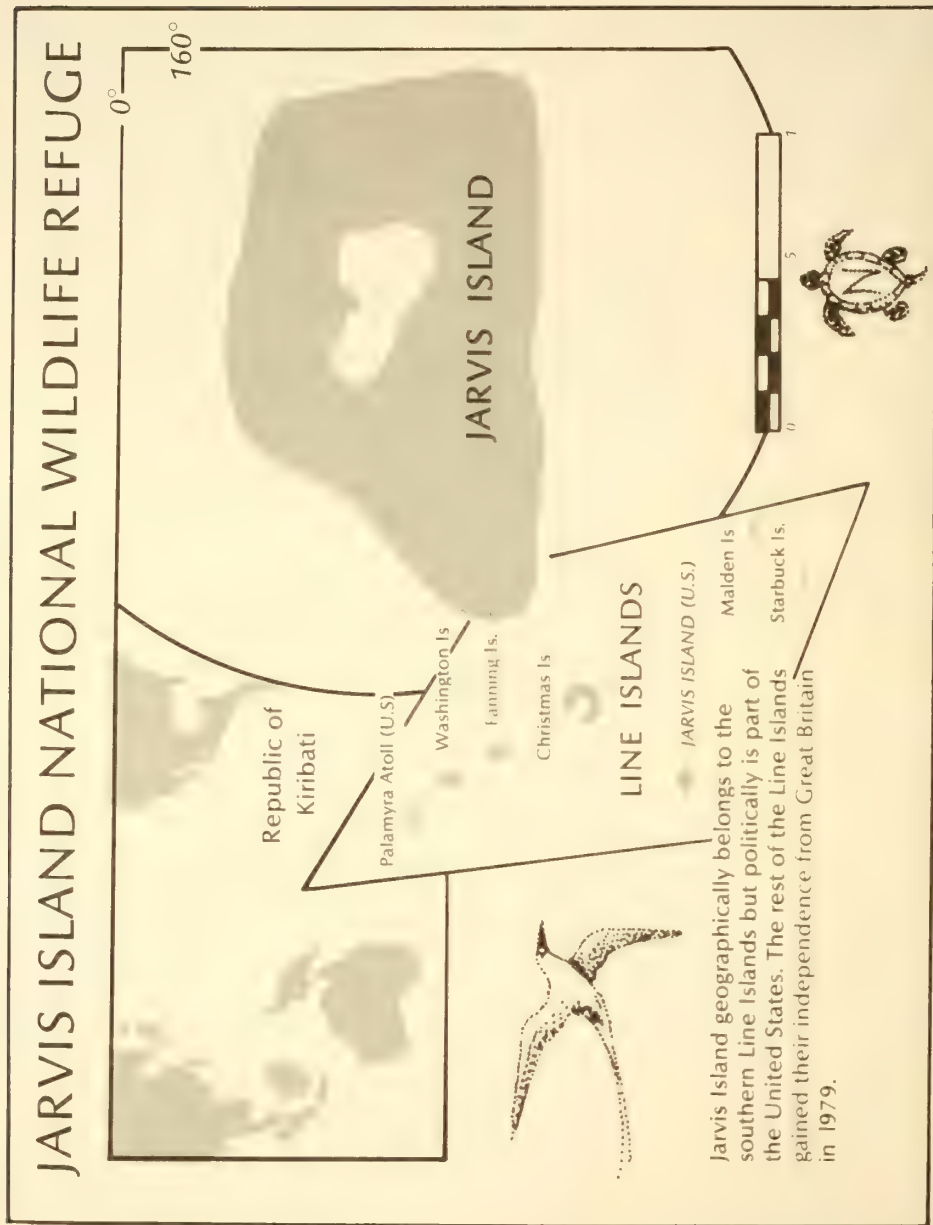


FIGURE 1

LOCATION OF JARVIS ISLAND

FERAL CATS ON JARVIS ISLAND: THEIR EFFECTS AND THEIR ERADICATION

BY

MARK J. RAUZON*

INTRODUCTION

Island ecosystems have proven to be particularly sensitive to human disturbances (Bourne 1975; Byrne 1980; Jarvis 1979). This was first noted by Charles Darwin in the explanation of his theory of natural selection (Byrne 1980). Since then, qualities of insular species have been examined by various authors in an attempt to understand the basis for island vulnerability.

Within island environments, there is generally less competition and predation than there is in corresponding continental habitats (Jarvis 1979). Introduced species are often competitively superior to insular species. However, the success of introduced species on oceanic islands can be attributed, in part, to human disturbance. The initial advantage of introduced species is their ability to withstand the types of disturbances associated with man (Egler 1942; Mueller-Dombois and Spatz 1972).

Of all the environmental changes caused by introduced species, predation has one of the most immediate effects on indigenous populations. Specifically, the feral cat (Felis catus) has played a major role in the eradication of native birds on islands. In New Zealand alone, these predators are implicated in the extinction of at least 6 endemic species and over 70 localized subspecies (Merton 1978).

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Research on Marion Island, a sub-Antarctic possession of South Africa, illustrates the potential magnitude of cat predation. By calculating the caloric needs of cats in all developmental stages and the caloric content of prey species, van Aarde (1980) was able to determine that 200 petrel-sized birds were eaten per cat per year. At least 455,119 birds had to be consumed to provide energy for the 2137 cats. Based on scat analysis of 375 cats on Macquarie Island, the yearly total of prey eaten are 56,000 rabbits (Oryctolagus cuniculus), 47,000 Antarctic prion (Pachyptila desolata) and 11,000 white-headed petrels (Pterodroma lessonii) (Jones 1977). Cats in the Kerguelen Archipelago probably kill about 1.2 million birds every year (Pascal 1980).

Returning a disrupted ecosystem to a condition more closely resembling the original state requires the complete removal of introduced species, especially predators. Even so, unanticipated results can occur. Attempts to eradicate rats which were endangering the Bermuda petrel (Pterodroma cahow) resulted in an increase of tropicbirds (Phaethon sp.) which colonized burrow nest sites formerly used by petrels. This problem was solved by fitting the burrows with baffles to exclude tropicbirds (Murphy 1964).

Eradicating introduced animals, even from relatively small islands, is a difficult and exacting task. This is particularly true in dealing with carnivores, which are capable of "... learned behavioral responses" (Beck 1975). Feral cats were eliminated from 8 islands in New Zealand. The complete removal of cats from Little Barrier Island spanned 4 years and involved 128 people and 3880 man-days (Veitch pers. comm.). A partial reduction of cats from Marion Island, South Africa, was produced by the introduction of feline panleucopenia virus followed by mechanical control efforts (van Aarde pers. comm.). I report here on the tentative eradication of feral cats from Jarvis Island, central Pacific Ocean.

JARVIS ISLAND

Jarvis Island ($0^{\circ} 22'S$, $160^{\circ} 01'W$) is a remote, emergent atoll located approximately 1300 miles south of Hawaii between the Line and Phoenix Island groups (Figure 1). The island is about 25 miles south of the equator and 200 miles southwest of the nearest island, Christmas Island, Kiribati. It consists of 1024 acres (about 1.6 square miles) of coral rubble, phosphatic guano and organic detritus (Bryan 1974; Hutchinson 1950). The desert-like climate is characteristic of atolls in the Equatorial Dry Zone which is bordered roughly by 5° latitude north and south. Slightly south of the equator and east of 180° meridian lies the minimum rainfall region which includes Jarvis (Taylor 1973). This scantily vegetated island is highly reflective of strong solar radiation which retards precipitation over the island even when rain is falling over the surrounding ocean (Christophersen 1927). Only 30 inches of rain fell during the five-year period from 1975 to 1980. A remote automatic weather station was operated for about 3-1/2 years during that time (Vitousek, Kilonsky and Leslie 1980). To the north of the minimum rainfall zone, Christmas Island receives about 30 inches of rain per year.

The scarce vegetation is typical of strand communities of the tropical Pacific and consists of Boerhaavia diffusa, Portulaca lutea, Sesuvium portulacastrum, Sida fallax, Tribulus cistoides, Lepturus repens, Eragrostis whitneyi and Abutilon indicum (Christophersen 1927). The location and areal cover of major plant communities is shown in Figure 2. A similar map was reproduced by E. H. Bryan in 1942 and comparison between the 2 maps (Figure 3) indicate few changes except in the degree of Tribulus cover, a phenomenon which appears to be seasonal (Bryan 1942).

The highest point of the island is the northwest beach crest which is approximately 25 feet above mean sea level. The topography indicates that Jarvis Island was once a horseshoe shaped atoll with a lagoon in the center. As the lagoon drained and filled, extensive beds of gypsum were formed (Hague 1862 in Hutchinson 1950; Jewell 1961). Continual deposition of seabird excreta created a valuable deposit of phosphatic guano.

Jarvis Island was discovered by Captain Brown of the British ship ELIZA FRANCIS on 21 August 1821. Various ships visited this island, also known at the time as Jervis or Bunker, before 1856 when it was claimed by the American Guano Company and the United States Guano

company under the U.S. Guano Act of 1856 which allowed ship captains to claim sovereignty over unoccupied islands. The U.S. government claimed that mere discovery did not give final title if not followed immediately by reasonable occupation. In February 1858, C. H. Judd took 23 Hawaiian laborers to begin mining guano (Judd 1960). Excavation of phosphatic guano lasted until 1879 (Bryan 1974). Initial estimates based on the vast numbers of seabirds present in 1856 predicted that 7 million tons of guano were available. However, log reports from commercial guano vessels indicate it was unlikely that the output exceeded 12,000 tons annually. By the termination of the lease in 1879, approximately 300,000 tons were removed from Jarvis Island making it one of the richest deposits in the Central Pacific (Hutchinson 1950). The ownership of Jarvis was contested when Great Britain annexed the island in 1889 and leased the deposits to the Pacific Phosphate Company of London and Melbourne. Because so little high quality guano remained, the lease was allowed to expire (Bryan 1974). Today, rows of low-grade spoil remain in 3 to 7 foot walls in the interior of the island providing dens for cats.

The value of Jarvis and other equatorial island possessions grew as trans-Pacific aviation became a reality. In 1935, Jarvis, Howland and Baker Islands were colonized with Hawaiian high school graduates. This action was followed by the Presidential Order 13.5 in 1936 re-establishing the claim to the islands as American territory (Bryan 1974). Great Britain then relinquished its claims (Leff 1940). The islands have since been administrated by the Department of the Interior and are now part of the Hawaiian and Pacific Islands National Wildlife Refuge system directly administered by the U.S. Fish and Wildlife Service in Honolulu, Hawaii.

Human occupation of Jarvis Island created changes in the simple ecosystem. Goats, rats, cats, mice and introduced plants like Abutilon indicum undoubtedly affected the native ecosystem (Bryan 1974; Christophersen 1927; Judd 1960). In 1885, no birds were seen during a survey in October-November. One cat was observed "in possession of a house" (MacFarlane 1887). The Whippoorwill Expedition of 1924 found many mice and seabirds but no cats (Gregory, 1925).

CATS ON JARVIS ISLAND

By 1935, goats and cats had been extirpated but Polynesian rats (Rattus exulans) were still abundant. "What we call 'field mice' [small Polynesian rats] by the dozen crawl over the beds during the night and sometimes get caught between the blankets." (Bryan 1974). If cats had become established in 1885, rats would not have been so conspicuous. The Hawaiian colonists were required to note relevant biological observations (Bryan 1974). The presence of cats would not have escaped their notice. However, cats are mentioned in the correspondence surrounding the death of Karl Kalawai on October 1938. Kalawai's contemporaries were required to write their version of his

death from appendicitis. In one letter, it was noted that the pet cat and dog were doing fine (Bryan 1974). It may be that the colonists brought cats, against orders, to prey on the disturbing number of rats. The cats may have escaped the confines of the camp and have become feral. King (1973) outlines the settlement of Jarvis and states that the settlers left cats when they abandoned the island.

During the International Geophysical Year 1957-58, the island was manned as a research station with scientists from Scripps Institute of Oceanography (King 1973). One scientist reported killing several hundred cats during his stay (R. Clapp pers. comm.). The Pacific Ocean Biological Survey Program (POBSP) visited Jarvis in 1964 and 1965 and they killed over 200 cats (King 1973). POBSP visits in 1967 and 1968 located only 9 cats in 2 days (King 1973). A visit in 1973 by the U.S. Bureau of Sport Fisheries, now the U.S. Fish and Wildlife Service, sighted at least 14 cats (Kridler 1973). Giezantner (1976) reported killing 12 cats and sighting 50 more on 2 surveys around the island in 1976. In 1977, 102 cats were shot and 50 to 75 remained alive. In 1978, 160 cats were shot, most of them kittens (Forsell 1978). These data suggest the carrying capacity is less than 200 cats.

Surveys conducted opportunistically by the POBSP and during subsequent eradication efforts have identified and partially defined the extent of cat predation. Rats were formerly abundant on Jarvis but were probably extirpated by cats (King 1973). Mice (Mus musculus) persist in varying numbers. The POBSP noted the largest populations of birds over 4 years from 1963 to 1966 (Table 1). Three species of birds continue to breed in substantial numbers. Masked boobies (Sula dactylatra) and red-tailed tropicbirds (Phaethon rubricauda) are relatively large birds capable of defending themselves and their young. Sooty terns (Sterna fuscata) breed in very large numbers and inundate the cat population with more food than it can consume, then depart en masse. Nevertheless, the cats' predatory effects are significant. On nearby Starbuck Island, a cat population about the same size as that of Jarvis killed about 1000 birds a night (King 1973). Subsequent bird surveys have not been as comprehensive as the POBSP work which makes comparisons difficult. However, gross changes are apparent. In spite of annual and seasonal variation, the most obvious trend appeared to be a precipitous decline to the point of extirpation of the red-footed booby (S. sula) and the frigatebirds (Fregata sp.). Only roosting birds were seen in 1982-83 though derelict nests were found. Small ground-nesting birds were absent. Surveys in November 1983 indicate that predation has ceased and may offer proof that cats have been eliminated.

METHODS AND MATERIALS

From June 14 to 27, 1982, a study of the ecology and behavior of the cats was undertaken by David Woodside of the U.S. Fish and Wildlife

Service (FWS) and myself. Radio telemetry was used to determine home range and to test the efficacy of feline panleucopenia virus as a possible control agent. From June 27 to July 10, 1982, eradication techniques were implemented while additional biological observations were made. Attempts were made from October 28 to November 3, 1982, by Woodside, Steven Fairaizl (FWS) and Utimawa Bukaireiti of the Christmas Island Wildlife Conservation Unit (CIWCU) to complete the eradication work using recommendations garnered from the first trip. From March 3 to 9, 1983, Woodside and Katino Teebaki (CIWCU) attempted to remove the final cat(s) from Jarvis Island. Cameron B. Kepler (FWS) searched for cats from November 6 to 10, 1983, without sighting any. His seabird observations indicate that cat predation has ceased and that cats may be absent from Jarvis Island.

RADIO TELEMETRY

Cats were captured using TOMAHAWK live traps set nightly with various baits. Traps were checked early each morning to avoid subjecting the animals to heat stress. When a cat was to be collared with a radio transmitter, it was removed from the trap by placing a burlap bag over one end. The trapdoor was opened and the cat was directed into the bag. After the bag was tied shut, it was weighed using a 5 kg PESOLA spring scale. The bag weight was subtracted to give the net weight of the cat. The bag was carefully opened and the cat's head positioned at the entrance of the bag. The head and neck were exposed while the body continued to be restrained. While the head was held in a gloved hand, the neck was fitted with a radio transmitter collar. The collar was measured and cut to the appropriate size allowing the cat adequate room to swallow. The ends of the collar were bolted and glued together. The exposed metal end of the collar was taped and covered with heat-shrink plastic tubing to prevent any moisture from interfering with radio transmission.

Seven cats were fitted with radio transmitters of distinct frequencies for individual discrimination. AVM radio transmitters were selected for their range of frequency within the assigned U.S. Fish and Wildlife Service bands (164.467 to 164.709 megahertz) as well as their 3-month battery life. The collar weighed about 25 g which is the maximum size a cat can carry without interfering with its ability to carry out normal behavior. The transmission could be received over a 3 km distance or line of sight. Complimentary receivers (AVM) powered by 8 AA DURACELL batteries were used in conjunction with YAGI 3-tined antennae compatible with the selected frequencies.

Radio checks were conducted twice a week by scanning the occupied channels. Compass bearings were taken of the maximum signal strength determined by standard pattern sweeps of the antenna (Cochran and Lord 1963). This single bearing technique sufficed when a general position was sought. Fixes were taken from 1 or 2 stations at known map locations and then plotted to determine a more exact position (Figure

4). However, some sources of bias and sampling error in this method of triangulation were sufficient to justify the more time consuming process of homing (Springer 1979). Homing was necessary to locate the den sites of inoculated cats. This technique is to follow the direction of the maximum signal strength as it audibly increases. By intermittently increasing the interference (the 'squelch' knob) as the signal audibly increased, we were able to hear nuances in the strength of the signal and hence, determine its directionality (Cochran and Lord 1963).

The nature of the radio signal indicated the activity of the cat. A signal that varies in strength indicates an active animal that is moving its head. A steady signal indicates a recumbent animal. The surrounding environment affected the nature of the signal as well. Dense coral slabs interfered with the signal to present a 'muffled' sound. Likewise, transmission around metal objects gave a 'bounce' which confused directionality.

FELINE PANLEUCOPENIA

Five cats fitted with radio transmitters were given an oral dose of 0.5 cc feline panleucopenia virus (FPLV) and released. Two cats were collared and released unexposed to FPLV as control animals. An additional 26 cats were inoculated, 19 of these were marked with spray paint and released (Table 2). Data from bi-weekly fixes were used to determine the areas to which FPLV might spread as well as to define home range, den site affinity and movement. Significant movement hastened the spread of the contagion and justified inoculating fewer animals.

Poole (1972) has shown that a modified live panleucopenia virus is stable at 37°C when stored in the medium in which it was produced for up to 5 months. Based on in vitro stability of the virus when stored at room temperature, we felt that the virus could retain virulence when stored without refrigeration at Jarvis Island. Since we were unable to hold cats in captivity to determine the dosage and potency of the virus, we used the radio-collared cats to provide these data.

BAITS

Bait attraction studies were conducted concurrently with live trapping to determine the most effective baits for this and future control efforts (Table 3). The first baits were chosen for their intrinsic attractiveness to cats. Several species of reef fish were initially tried. Gray mullet (Mugil cephalus), 'aholehole (Kuhlia sandvicensis) and manini (Acanthurus triostegus) were used as baits for 80 trap-nights. The fish were halved and partially scaled to enhance their attractiveness to cats.

In order to determine if traps were affecting the attractiveness of baits, a series of bait trials was established. Each evening for one week, 2 fish baits were set at least 10 feet from each other at 9 designated bait stations. Any evidence of visitation or fish consumption was recorded. Canned cat food (CALCAN; 'simmered supper', liver and fish) and canned sardines were also tested. A series of 6 open cans were placed at bait stations away from the traps. Station areas were cleared to detect cat footprints. Tincture of catnip was used as a lure in spite of previous low success rates (van Aarde pers. comm.). Twenty drops of catnip were placed on a small cloth bag stuffed with grass (Lepturus repens) to aid fragrance dispersal. Finally, the attractiveness of freshly killed sooty terns which were cut in half and set at bait stations was determined. During the second trip, feline gland lure was used on steel and CONIBEAR 220 traps. This experimental lure was made from the testes and urine of male cats.

POISON

After 14 days had elapsed, chemical and mechanical control methods were initiated. Because the use of the effective predicide 1080 is banned on federal lands, 3 experimental compounds and 2 known toxicants were cage bioassayed in Hawaii in order to determine a suitable alternative (Fellows 1982). Based on these results, the compound N-(3-chloro-4-methylphenyl acetamide) or CAT was chosen for field testing. It was imperative that CAT hold no secondary poisoning potential for scavenging birds or invertebrates. A series of cage bioassay tests were conducted with 7 captive hermit crabs (Coenobita perlitus). Fifty grams of dry cat food was mixed with seawater and 90 mg of CAT. This yielded a toxicity of 0.18% Active Ingredient (AI). The crabs were held for 3 days in a shaded chicken wire cage and fed this mixture and water. The experiment was repeated with 3 groups of 6 crabs. The control group received 50 g of cat food and water. The second group received 50 g of moistened food with 90 mg (0.18% AI) of CAT. The third group received moistened food with 180 mg (0.25% AI) of CAT. All groups were held for 3 days and released. The control group was unmarked, the second group was spray-painted orange and the third was spray-painted blue.

Approximately 50 g of sooty tern flesh rubbed with 90 mg of CAT constituted the LD₅₀ or lethal dose required to kill 50% of the cats upon first ingestion. Thirty pieces of freshly killed sooty tern were smeared with 50 mg of CAT and placed in open trays in the quarry area on June 27. Signs of visitation were noted the following morning. On July 10, the day prior to our departure, 20 pieces of sooty tern bait were placed in and around the burrows of wedge-tailed shearwater (Puffinus pacificus) which were also used by cats.

TRAPPING

In order to capture gun-shy cats, 2 other styles of traps were used. Steel or 'gin' traps designed to capture the cat by the foot were used in situations when the trap could be camouflaged. Lethal CONIBEAR 220 traps were set in den site entrances to trap cats as they entered or left.

To determine the density of house mice on Jarvis Island, a line of snap-traps baited with peanut butter was set in the quarry area within a microhabitat of Lepturus repens and around the camp at the north coast. The 3 traps at camp were caged inside chicken wire to exclude hermit crabs. An additional 17 were set without wire cages since hermit crabs are largely absent from the quarry.

Kepler (1984) attempted to census the house mouse population by counting mice on 5 transects covering an area of approximately 16,000 ft².

HUNTING

Hunting has played a major role in the eradication of cats from numerous islands in New Zealand (Veitch 1980) and South Africa (van Aarde 1980). Its effectiveness is enhanced when used in conjunction with a battery of other control measures (Beck 1975). Night hunting began on 27 June 1982 and continued until 10 July. Since cats are primarily nocturnal, headlamps powered with 2 D cell batteries were used to illuminate the horizon and create 'eyeshine,' a reflective response from the inner layer of the cornea of nocturnal animals. This is visible as a blue or orange glow from about 50 m away on dark nights. Ambient moonlight diluted the reflective response. On the second visit, which coincided with a full moon, more powerful spot lights were used. Night hunting was done with a Q-BEAM and SL-20 rechargeable hand-held spotlights. The SL-20's were taped to the barrels of the guns to facilitate sightings. A REMINGTON 12 gauge shotgun, single barrel with a modified choke using No. 2-3 shot for ample pattern spread and stopping power, was used primarily at night. Cats were shot during the day with a 0.22 mm calibre rifle fitted with a 4 by 40 telescopic sight using long hollow point ammunition. Post-mortem data collected from each cat include weight, sex, color, reproductive condition (in females) and stomach contents (Table 4).

BIRD CENSUSES

A census of nesting birds was made to determine what effects the removal of predators would have on population numbers. Comparison with earlier POBSP data allowed population trends to be identified (Table

1). Estimates of nesting sooty terns were made by measuring four 10 meter square plots and counting all the enclosed eggs. Simple counts of masked and brown boobies (S. leucogaster), wedge-tailed shearwaters and red-tailed tropicbirds were also made in 1982. Other non-breeding birds were censused as they arrived. The population estimates represent maximum numbers. Kepler (1984) censused birds in November 1983 using a series of transects. His work will allow repeated comparisons on future expeditions.

RESULTS AND DISCUSSION

RADIO TELEMETRY

The results of the telemetry study indicate that the radio-collared cats remain in specific den sites during the hottest part of the day and become active at dusk (Figure 4). The principal feeding area on Jarvis Island was located along the south shore away from any known den sites. Panaman (1981) reports that within the home range, cats attempt to cover droppings but outside the home range, droppings remain exposed. Several high-density areas of cat droppings were found in the middle of the island well away from any suitable den site cover. It may be that the north shore cats cross the island to feed and while in transit, pause to mark these sites. No dropping sites were found in known home ranges of collared cats.

The home range was determined by plotting the fixes taken by homing and triangulation. Some positions taken by triangulation may be in slight error. Also some signals were not received during fixes. The female cats (nos. 3, 4, 7, 9) were consistently tracked to specific dens. Cat No. 3 used the periphery of the guano quarry as a home range (Figure 4). Cat No. 4, a lactating female with a small kitten, used the southern portion of the quarry. This area had dense Lepturus and loose ground for cover. Cat Nos. 7 and 9 inhabited the coral slabs of the north coast. There appeared to be considerable movement along this coast. No. 7 was also recorded in the quarry by a questionable fix. The home range area surrounding the den site is larger for males than for females (Macdonald and Apps 1978). The male cats (Nos. 6, 8, 11) were located in various den sites. Cats 6 and 8 were once recorded sharing the same den at the same time in the quarry area. Cat 8 was recorded mostly from the north east coast but was killed in the quarry accompanying cat No. 4.

It may be that the lack of suitable dens forced cats to share. One den in the quarry was occupied by at least 2 males, 2 females and one large kitten during the observation period. Although no cats were recorded near the southern sooty tern colony, it is clear from stomach analysis that the cats move freely across the island to feed on terns.

Veitch (1980) found cats on Little Barrier Island had a variable home range depending on the proximity of the feeding area.

FELINE PANLEUCOPENIA

We felt the spread of the contagion FPLV was likely because cats seemed to co-habit sites. Transmission of FPLV usually occurs by direct contact between the infected and the susceptible cats via saliva, feces, urine and fleas (Kahn 1978). In fully susceptible cats, i.e., those without active immunity, termination of the disease, either by death or by recovery is from one to 10 days (Veitch 1982). Death may occur at any stage after the rise in body temperature, however, it usually occurs after 2 to 4 days of manifest illness. The virus creates severe hemotological changes by destroying the blood-forming tissues. There is a gradual fall in the white blood cells, followed by dehydration. Recovery is characterized by a rise in white blood cells and the appearance of antibodies. It takes the animal several weeks to regain normal body weight but it will have acquired active immunity for up to 4 years (Gaud and Hallauer 1976; Veitch 1982). Feline panleucopenia is present in feral cat populations of most large areas. The disease tends to gradually build up to epidemic proportions and spread to all susceptible individuals before it dies out. Islands are usually too small to harbor reservoirs of the virus, so once it has passed through a population, it will die out. We believed the cats on Jarvis may have been exposed to the virus many years ago but were again susceptible.

The virus appears to have had a significant effect on the population. Cat No. 3, a female, died within 10 days of receiving an oral dose of FPLV. She exhibited the clinical symptoms of mucal discharge about the eyes and nose. She was located via telemetry at the periphery of the quarry appearing sluggish and listless. The next day she was found dead in the open grass. The remaining 4 radio-collared infected cats were allowed to live up to 18 days before it was necessary to kill them. No further expression of FPLV was noted. During the hunting phase, 10 out of the 19 marked and infected cats were shot. All appeared healthy with excess fat stores in the peritoneal cavity and displayed glossy coats and well-developed teeth. However, 9 of the 19 were not resighted. It may be that these cats died from the disease and went unnoticed. It is also possible that these cats were among those shot at night and not recognized because the marks rubbed off. The possibility that these cats represent additional FPLV mortality must be considered in light of the data presented by Scott, et al. (1970). He reports that about 50% of the challenged cats will expire. Van Aarde (pers comm) has used FPLV to reduce the cat population of Marion Island by 54% within 2 years of initial exposure. His most recent survey (May 1980) indicated a further 65% decrease with no indication of immunity build-up. At Jarvis Island, we felt that mortality would be above 50% since the xeric climate would hasten dehydration. The mean daytime temperature of

95°F may have affected the virulence of the virus in spite of Poole's (1972) suggestion that the virus could survive at 99°C. At best, we had a 41% mortality of marked cats (Table 2).

Veitch (1980) concluded that FPLV did not work well enough to justify the trapping effort needed to inoculate at least 5% of the population to spread the contagion. In areas with dense cover, it is very difficult to determine the extent of mortality necessary to justify its continued use in lieu of more conventional control methods.

BAITING AND TRAPPING

Baits are used either to lure cats into traps or to carry poison (Veitch 1982). Fresh fish is a readily available bait on islands so we began to trap cats using fresh reef fish (Table 3). In the 80 traps that were set, 11 cats were captured (14% success rate). Concurrently, 18 pieces of fish were set outside of traps to see if cats avoided the traps. Only 2 pieces (11%) appeared to have been visited by cats. Canned cat food and sardines were tried as bait in 12 traps but no cats were captured. Even at 18 bait stations outside of traps, there was no evidence of cat interest. Tincture of catnip was used in 4 traps also without success.

Sooty terns appear to be the most attractive bait judging from trapping results. Before hunting began, 64 traps were set with terns and 25 cats were captured (39%). After hunting, 40 traps were set and 4 cats were captured (10%). The relatively high success rate of 39% led us to choose terns as the main bait for trapping and poisoning efforts. Overnight, all baits became infested with Oedemerid beetles (Ananca bicolor) which greatly reduced their attractiveness. However, day-old sooty tern pieces still held some attraction. This was an unexpected lure since felids do not readily accept carrion as bait (Beck 1975). Two cats were captured with this bait and several others showed interest by pulling the feathers which protruded from the cage until the meat was in contact with the wire mesh. Some fresh baits were partially consumed in this manner. This learned behavior may indicate trap avoidance. Only 2 marked inoculated cats were recaptured, although unmarked inoculated cats may have been. Using all combined baits, 200 traps were set and 40 cats were captured (20%). It is instructive to compare the trapping effort at Little Barrier Island, a heavily forested and highly eroded island, with that at Jarvis. In 1977, 2637 traps were set and 26 cats were caught. In 1978, 37,332 traps were set and 73 cats were caught. In 1980, the last year of trapping, 32,615 traps were set and only 5 cats were caught (Veitch 1982).

Trapping success is a function of population size and the experience of the trappers. As animals become more scarce, the success in trapping declines at roughly an exponential rate. In order to trap experienced animals, we used 2 other styles of traps, leg-holds and

CONIBEARS. These traps would have had a higher success rate if used earlier in the eradication campaign. Since these traps were not baited, they were placed in areas that animals frequent, like denning sites or runways. Leg-hold traps were placed in entrances and along runways blocked with fencing which detoured the cat into the traps. During 49 trap-nights, one cat was caught (2%). CONIBEAR 220 traps are even more site specific since they must be supported externally. Seven traps were placed in the entrance to dens. Two cats were killed. Two red-tailed tropicbirds were caught and killed while exploring potential nest sites. These were the only cases of non-target vertebrate mortality.

During the October-November trip, feline gland lure was used in addition to various baits such as booby meat and cooked fish. In spite of the lure's previous success in mainland situations, no cats were caught. This is probably a result of very low population densities.

In attempting to estimate rodent population density, 46 snap-traps were set in the quarry. No mice were caught. In traps without a chicken wire enclosure, 4 land crabs were caught. Three traps were set at camp where mice were previously seen. Two were caught.

POISONING

Since hermit crabs are potential subjects for secondary poisoning by scavenging, a series of toxicity tests were initiated on 18 June with 7 crabs. The crabs received cat food mixed with 0.18% AI CAT. They were not observed eating the bait during the 3 day trial. They appeared listless and hung upside-down in the cage after repeated escape attempts failed. They were released and the food was exposed to free-roaming crabs who quickly consumed it. It appeared that the listless behavior was a response to captivity.

This experiment was repeated with 3 groups of 6 crabs. A portion of the poisoned bait was consumed by 2 groups. The crabs again appeared listless. One individual shed its shell and escaped through the wire mesh. The spray-painted crabs which had consumed bait with 0.18% and 0.25% AI CAT were released and subsequently resighted one week later along the beach. It appeared that these concentrations of CAT were not lethal to hermit crabs. These data are essential if aerial broadcasting of poisoned bait is considered as a future control method.

Thirty 50 g pieces of sooty tern were poisoned with 0.18% CAT (Table 3). The following morning, 15 pieces (50%) remained untouched. Five pieces (16%) were moved but not eaten. Nine pieces (30%) were partially eaten and one piece was wholly removed. Two days later, this test was repeated with 28 pieces. Seventeen (60%) were untouched. Two (7%) were moved but not eaten. Two were partially eaten and 7 (25%) were removed. The relatively high rate of consumption (33%) approaches

the rate of trapping success using sooty terns. In addition, 28 pieces of poisoned bait were placed in and around shearwater burrows occupied by cats. The effect of the baits is unknown. No carcasses of poisoned cats were found. Veitch (1980) reports similar findings. At least 26,850 pieces of bait were placed on Little Barrier Island, but only 4 carcasses were found.

Fellows (1982) determined in test animals that the mortality rate was about 75% in cats that consumed at least 13 mg of CAT per kg of body weight. Assuming that only half of the 50 g bait (0.25% AI) was consumed, it would have delivered a lethal dose to the heaviest cat on Jarvis Island (Table 4). Death from CAT is due to renal failure (Palmore 1978). Like FPLV, it was hoped that the xeric climate might increase mortality. During the study, rainfall was sporadic, yet sufficient quantities collected in the shells of the giant clam (Tridacna maxima) to provide a constant supply.

HUNTING

The number of cats shot during the 1982 hunting period is plotted in Figure 5. The number of cats shot per day is plotted along the Y axis with the number of hours hunted per day. The number of hunting days is plotted along the X axis. The obvious trend is initially high mortality with a quick drop-off as hunting progresses. The number of hours hunted per day is the man-hour effort. As targets become fewer, man-hours to hit those few targets increases. The first 7 days of hunting yielded 1.97 cats per man-hour of hunting. The yield for the second week was only 0.19 cats per man-hour. The total yield for 110 man-hours of hunting was 105 cats or about one cat per hour of hunting from a population of about 44 cats per km².

Past eradication efforts on Jarvis Island have been brief though targets numerous. Thus a high rate of depletion was obtained by Forsell (1977, 1978). He shot 5 cats per man-hour in 1977 for a total of 102. He estimated that 50 to 75 cats remained alive. In 1978, he and a group of U.S. Coast Guardsmen shot 4 cats per man-hour to reach a total of 160. With the same manpower on Howland Island, the hunting kill was only 0.8 cats per man-hour in 1977 and 0.14 in 1978. The latter rate approximates that in our attempt to shoot the last Jarvis cats. On the October 1982 trip, Woodside spent over 100 hours to shoot two cats. In March 1983, over 100 hours were hunted without success. At least one cat was sighted (Woodside pers. comm.). In June 1983, an experienced hunter reported seeing no cats during 2 days of hunting (Austin pers. comm.). Kepler (1984) hunted for 35 hours over 4 days without seeing any sign of cats, i.e., eyeshine or predated birds.

Hunting on the Kerguelen Archipelago halved the maximum lifespan and lowered the population age as well as caused a disequilibrium in

the sex ratio. Hunting reduced the geographical range of the cat population (Pascal 1980). On Marion Island, van Aarde (pers. comm.) reported; "Under sub-Antarctic conditions with population density of approximately 10 adult cats per km², a success rate of 2.5 hours per cat (0.4 cats per hour) was achieved. This efficiency decreased roughly exponentially with a decrease in population density." Both Marion and Jarvis Islands are relatively clear of vegetative cover so hunting can be used effectively. On the well-vegetated Little Barrier Island even hunting with dogs was futile.

BIOLOGICAL POPULATION CHARACTERISTICS

Hunting provided the opportunity to examine the biological characteristics of the Jarvis Island cat population as a whole (Tables 4 and 5). The color and sex of 108 cats were recorded. Black females were the most common phenotype (33%) followed by black males (25.5%). Black cats composed 58.5% and tabby cats composed 31.5% of the population. While live-trapping, we noted that black cats caught in traps and exposed to the morning sun appeared listless and frothy at the mouth, but lighter tabby cats showed no ill effects. The black cats possibly experience more heat stress from high solar radiation than the lighter tabby cats. Van Aarde (1980) hypothesized that dark coat color may have some advantage in the sub-Antarctic and that a strong founder effect is indicated by the absence of piebald spotting. On Jarvis, only 2.1% of the cats were piebald. On the Kerguelen Archipelago, the feral cat has kept the principal dark color characteristics of the domestic cat for over 20 years (Derenne 1976). Dark cats may be more successful nocturnal hunters than lighter ones.

Relatively small sample sizes prevent any conclusions from being drawn but some interesting trends are apparent. Overall, the sex ratio is roughly equivalent; 52% females, 48% males. This difference is not significant ($P < 0.5$). However, the gray cats show a highly significant ($P > 0.02$) sexual bias to males (9:1). Piebald cats were the least common phenotype represented by 2 males and one female. The other non-gray cats were at least 95% black.

The weights of 42 adult cats fell within the normal range for the common domestic cat (Scott 1972). Tabby males were on the average the heaviest but the heaviest individual was a black male. The weights of both sexes were heavier than those reported from Raoul and Little Barrier Islands in New Zealand and lighter than those from Herekopare and the sub-Antarctic Macquarie Island (Veitch 1982, Jones 1977).

DIET

Of the 54 cat stomachs examined, 32 (59%) contained flesh and feathers of sooty tern adults and embryos as well as eggs. A subcolony

of terns near the main colony was heavily predated. Small teeth marks on eggs indicated that cats fed on them. The colony was later deserted en masse. Although terns are known to desert colonies, especially in vulnerable peripheral areas, it would appear that predation is an added pressure to desert (Ashmole 1963). Stonehouse (1962) found that cats on Ascension Island rarely ate sooty tern eggs however there are records of cats eating eggs of grey-faced petrels on Kerguelen Island and dominican gulls (Larus dominicanus) on Dassen Island, Southeast Africa (Atkinson pers. comm.). Eggs may be a learned food source selected only by a few cats in some colonies.

Analysis of stomach contents showed that twenty one stomachs (38%) were empty. Since sooty terns settle on the ground after dark, the absence of food in these cats could indicate that night hunting had not yet begun. Also, during our hunting phase, the moon was full. Presumably, terns would be harder to catch on brightly lit nights and so the cats would be less successful. Since sooty terns are the primary food source, it is reasonable to assume that they limit the cat population. Stonehouse (1962) suggested that cats on Ascension Island are also limited by the nature of the tern breeding cycle. There is no shortage of food when terns arrive. When the breeding cycle is complete and they leave, cats are forced to survive on less easily obtained food.

One red-tailed tropicbird chick was identified in a cat stomach. A deserted masked booby chick was observed being stalked by a cat. It was later missing. The remaining 3% of the stomachs contained parts of crickets and cockroaches. Fitzpatrick (1979) found many species of invertebrates in cats which indicated a seasonal dependence on this food supply. One gecko was also identified in the remains. In spite of the abundance of reef fish, only one cat had fish in its stomach. These were probably prey items from a sooty tern which itself had subsequently been consumed. It may be that the abundant hermit and ghost crabs effectively compete for the carrion of the beach.

The last cat shot during the June/July trip had one mouse in its stomach. Several months later in October, one of the 2 cats shot had 5 mice in its stomach. During the March 1983 trip, mice were reported as very common in contrast to earlier trips. This increase in mice is almost certainly related to the decreased predation pressure. In November 1983, mice were conspicuous and possibly undergoing a population crash. A rough estimate of 36,000 mice on Jarvis represents an order of magnitude figure (Kepler 1984). During the Whippoorwill Expedition of 1924, mice were abundant (Gregory 1925). In 1935, mice were still abundant (Bryan 1974). In quoting the journals of the colonists, Bryan inserted in parenthesis that mice were Polynesian rats; "What we call 'field mice' [small Polynesian rats] by the dozen crawl . . ." (Bryan 1974). If this were true, then the introduced cats eliminated the rats but not the mice. However, it may be that the mice eliminated the rats since evidence from Stewart Island, New Zealand, suggests that mice are able to exclude ecologically Polynesian rats from a grassland biome (Taylor 1975). In other tropical regions,

Polynesian rats do co-exist with mice but Jarvis Island may be such a simple ecosystem that this is impossible (Storer 1962; Tomich 1970).

FECUNDITY

During the hunting phase, 5 kittens were shot. This represents a relatively low recruitment rate which may be influenced by the lack of a steady food supply prior to the arrival of sooty terns. During late May 1982, terns began to arrive. Their arrival may have stimulated the onset of oestrous as evidenced by the apparent increase in pregnancies and the number of kittens in-utero. Of the 26 females examined, 8 were pregnant. The average number of embryos was 3. The survival rate of kittens is unknown but at least 24 could have been born.

BIRD POPULATIONS

Four 10 m by 10 m quadrats within the sooty tern colony were censused. The mean density of eggs was 37 per 10 m². We then measured the roughly linear colony to determine the area and multiplied that area by the mean egg density to determine that 210,000 eggs or 444,000 nesting birds were present. We estimated that an additional third of the colony were nonbreeders. Near the western and eastern beaches were 2 more colonies (Figure 4). Approximately 500,000 additional birds were present bringing the estimated total population of sooty tern to over 1 million birds.

Stonehouse (1962) considers the predatory effects of even 100 cats to be considerable. If the cat population is about 120 on Jarvis Island, and each cat eats a bird a day for about 200 days; the average period a colony might be established, then the annual cumulative predation could approach 25,000 birds per year or about 2.5% of the total sooty tern population.

The masked booby colony is one of the largest in the Central Pacific Ocean. King (1973) estimated that 9000 individuals were present. Our estimates of breeding birds agree but are slightly less for nonbreeding birds (Table 1). This species is loud and aggressive and apparently suffers little cat predation. Likewise, the red-tailed tropicbird is well-defended. King (1973) recorded "large populations of both frigatebirds and all three boobies. . . ." In 1982, about 1550 lesser frigatebirds and 550 red-footed boobies roosted in the center of the island at night. These birds were not breeding on Jarvis in 1982 and may be considered victims of cat predation. One partially consumed booby was found in the quarry well away from the roost site. In addition, less than 50 brown boobies and 10 wedge-tailed shearwaters breed on Jarvis Island. Other petrels, shearwaters and small terns are absent. A wing of a white-throated storm-petrel (Nesofregata

albigularis) was found on Jarvis Island indicating that this species may still visit and be a potential colonist.

Kepler (1984) found increased numbers of birds present during his November 1983 surveys conducted at approximately the same time as in the previous year (Table 1). He found 4 lesser frigatebird colonies with chicks. The largest colony (286 pairs) was only 50 m east of the guano quarry where cats were common in 1982. Red-footed boobies were breeding in small numbers. Kepler found 2 colonies, one with 15 nests, the other with 7 nests. Over 800 roosting birds were counted at night. Four separate sooty tern colonies were found out of synchrony with each other. Kepler attributes this to the species recovery from the effects of the El Nino that began in August 1982 (Firing et al. 1983).

CONCLUSIONS

Jarvis Island is considered to be of outstanding importance for the abundance of its wildlife especially breeding seabirds. The elimination of feral cats will probably make Jarvis Island one of the largest seabird colonies in the central Pacific Ocean (King 1973). Currently, the island is administered as part of the U.S. National Wildlife Refuge System by the U.S. Fish and Wildlife Service. Beginning in 1973, the Service attempted to eradicate the Jarvis cats by using sporadic control measures. In 1981, a systemic analysis of available control options and a survey of the results from other cat eradication work was conducted. As a result of this preparation, we investigated the use of feline panleucopenia virus as a control agent. Research in other insular situations suggest this technique could be helpful in reducing a susceptible population by at least 50%. By determining the home ranges and movements of cats using radio telemetry, we were able gauge the potential spread of the virus through the population. Only one radio-collared cat was killed by the virus. Additional deaths may have occurred to marked cats that were not subsequently recovered. If so, then the total mortality via FPLV was, at best, 41% of the inoculated cats. Nevertheless, we judged this technique to be relatively ineffective in lieu of other control measures which allowed full accountability of mortality. Accountability is essential, especially in the case of Jarvis Island, when visits are infrequent and of short duration.

Poisoning was another indeterminate technique particularly because experimental compounds were used. The current controversy surrounding the use of compound 1080 on federal lands prevented us from obtaining this effective toxin. However, bioassays conducted in Hawaii and on Jarvis Island have indicated that CAT is an effective control agent for cats and does not hold any secondary toxic effects for scavenging invertebrates. Aerial baiting could be possible with this toxin.

The combination of hunting and trapping proved most useful in removing the majority of the cats from the island. However, the success of these methods is limited by the amount of manpower available. As targets become fewer, the effort must correspondingly increase if the last cats are to be shot or trapped. This effort can become very costly, time consuming and frustrating especially if time is limited. On Jarvis Island, the last 250 man-hours of hunting removed only 2 cats.

Trapping efficacy is also affected by the population density of animals. After one week of hunting, the capture rate decreased from 39% to 10% while using terns as bait. A variety of baits were tested to determine the most attractive. Familiar foods, i.e., terns and fish (to a lesser degree), attracted all the cats that were trapped. The use of feline gland lure was ineffective but might succeed when baits fail during periods of abundant prey. Steel leg-hold and CONIBEAR 220 traps were useful and could have caught more cats if used earlier in the eradication effort. They could be effective in removing the last cats provided ample time was available. It is essential to use all available methods over a reasonable period of time to provide a broad front of eradication techniques to remove the last wary cats.

The ability to account for the carcasses of cats afforded an opportunity to survey the phenotypic expression of an entire population. The observation that the majority of the population is black suggests some adaptation to the environment. In spite of the black cats' susceptibility to heat stress during the day, they may be less conspicuous than the other phenotype when hunting at night. All cats examined appeared healthy with sleek fur and adequate fat deposits. The weights of the cats fell within the normal range for the domestic house cats, and in fact were heavier than temperate climate cats from New Zealand.

Ecologically, Jarvis Island is severely changed. The miners who removed 300 thousand tons of guano initially altered the simple ecosystem with introduced goats, rats and mice. Yet seabirds were able to continue to utilize the island as a nesting ground until the introduction of cats. Cats allegedly extirpated the smaller nesting species which occur on similar tropical islands without predators. It was the purpose of this eradication effort to remove the cats in the hope that these species of seabirds, which are threatened by predators on many other islets through the Pacific, would return to colonize Jarvis Island. Future surveys will be needed to identify the extent of recolonization and to monitor the status of introduced species.

In attempting to rid the island of cats, we tried various established and novel techniques. In 1982, we removed about 120 cats but were not successful in complete eradication in spite of 6 weeks of effort involving 5 people. However, it appears that very few, if any, cats remain. The first major nesting effort by lesser frigatebirds in 2 years suggested that the cat population has either been eradicated or is very low and probably not breeding. If the population contains one

pregnant female, the population could rebuild its numbers in a brief period. We are not safe in assuming complete eradication until 4 or 5 years have passed with no cat signs. The threat of future cat or rat introductions is always present so long as ships pass by the island. The remoteness of Jarvis Island makes protection efforts very difficult.

Habitat rehabilitation is the responsibility of agencies in charge of administering disturbed lands. In the end, it remains the duty of the U.S. Fish and Wildlife Service to monitor the effects of eradication on Jarvis Island. To return disturbed ecosystems to a more natural state is a difficult task. Yet, every effort must be made to erase the deleterious effects that animals introduced by man have wrought. It must be stressed that man was the initial source of the introduced cats on Jarvis Island. Thus, it is our responsibility to remove them so the island can once again become a predator-free colony for many species of tropical seabirds.

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LITERATURE CITED

- Aarde, van R. J. 1980. The diet and feeding behavior of feral cats (Felis catus) at Marion Island. S.-Afr. Tydskr. Natuurnau. 10:3-4.
- _____. 1980. Gene frequencies in feral cats on Marion Island, South Africa. J. Hered. 5:366-68.
- Ashmole, N. P. 1963. Biology of the wide awake or sooty tern (Sterna fuscata) on Ascension Island. Ibis. 103b (3):297-362.
- Beck, J. (ed.). 1975. Use and development of sodium monofluoroacetate (1080) as a predacide. ASTM. 27-33.
- Bourne, W. R. P. 1975. Mammals on islands. New Scientist. 165:422-425.
- Bryan, E. H., Jr. 1942. American Polynesian: Coral Islands of the Central Pacific. Tongg Publishing Co. Honolulu, HI 253 pp.
- _____. 1974. Panala'au memoirs. Bishop Mus. Press. Honolulu, HI. 249 pp.
- Byrne, R. 1980. Man and the variable vulnerability of island life--A study of recent vegetation change in the Bahamas. Atoll Research Bull. No. 240. 200 pp.
- Christophersen, E. 1927. Vegetation of Pacific equatorial islands. Bishop Mus. Bull. No. 44. Whippoorwill Expedition #2. 71 pp.
- Cochran, W. W., and R. D. Lord Jr. 1963. A radio-tracking system for wild animals. J. Wildl. Mgmt. 27:9-24.
- Derenne, P. 1976. Notes on the biology of feral cats from the Kerguelen Archipelago. Mammalia. 40(4):531-95.
- Egler, F. E. 1942. Indigene verses alien in the development of arid Hawaiian vegetation. Ecology. 23:14-23.
- Fellows, D. 1982. Candidate cat control agent bioassay. U.S. Fish and Wildlife Damage Research Station, Hilo, HI 16 pp.
- Firing, E., R. Lukas, J. Sadler and K. Wyrski. 1983. Equatorial undercurrent disappears during 1982-1983 El Nino. Science 222(4628).
- Fitzgerald, B. M., and B. J. Karl. 1979. Foods of feral house cats in the forests of the Orongorongo Valley, Wellington. N.Z. J. Zool. 6:107-126.

- Forsell, D. 1977. Expedition report 1977. U.S. Fish and Wildlife Service Refuge Division, Honolulu, HI.
- _____. 1978. Expedition report 1978. U.S. Fish and Wildlife Service Refuge Division, Honolulu, HI.
- Gaud, S., and C. Hallauer. 1976. The parvovirus. Virology Monographs. Springer-Verlag. Wien, New York.
- Gregory, H. E. 1925. Report to the director for 1924. Bishop Mus. Bull. #21. Honolulu, HI. 55 pp.
- Giezentanner, J. B. 1976. Expedition report: Jarvis Island. U.S. Fish and Wildlife Service Refuge Division, Honolulu, HI.
- Hague, J. D. 1862. Phosphate islands of the Pacific Ocean. Amer. J. Science. 34:224-243.
- Hutchinson, G. E. 1950. The biochemistry of vertebrate excretion. Bull. Amer. Mus. Nat. Hist. 96:255-276.
- Jarvis, P. T. 1979. The ecology of plants and animal introductions. Prog. Phys. Geog. 3:187-214.
- Jewell, H. G. Jr. 1961. Preliminary report on the marine mollusca of the Line Islands. Haw. Shall News. 9(3):5, (4):1-7.
- Jones, E. 1977. Ecology of the feral cat (Felis catus) on Macquarie Island. Aust. Wildl. Res. 4:249-262.
- Judd, A. F. 1960. The guano islands: diary of A. Francis Judd, Voyage to Jarvis Island, 1858. Honolulu, HI. 105 pp.
- Kahn, D. E. 1978. Pathogenesis of feline panleucopenia. J. Amer. Vet. Med. Assoc. 5(2):628-630.
- Kepler, C. B. 1984. Jarvis Island report. U.S. Fish & Wildlife Service Research Division. Kula, Maui, HI.
- King, W. B. 1973. Conservation status of the birds of Central Pacific Islands. Wilson Bull. 85(1):89-103.
- Kridler, E. 1973. Ascertainment report. U.S. Fish and Wildlife Service Refuge Division. Honolulu, HI.
- Leff, D. N. 1040. Uncle Sam's Pacific islets. Stanford Univ. Press. Stanford, CA. 71 pp.
- MacFarlane, J. R. H. 1887. Notes of birds in the western Pacific, made in H. M. S. 'Constance,' 1883-85. Ibis. 201.

- Macdonald, D. W., and P. J. Apps. 1978. The social behavior of a group of semi-dependent farm cats, (Felis catus): a progress report. Carnivore Genetics Newsletter. 3:256-268.
- Mueller-Dombois, D., and G. O. Spatz. 1972. The influence of feral goats on the lowland vegetation in Hawaii Volcano National Park. US/IBP Island Ecosystems. IRP Tech. Rept. 13. 46 pp.
- Murphy, R.C. 1964. Discussion: conservation. In: Arctic-Antarctic Biology. R. Carrisk (ed.) Herman, Paris.
- Pascal, M. 1980. Structure and population dynamics of feral cats in the Kerguelen Archipelago. Mammalia. 2:161-82.
- Palmore, W. P. 1978. Diagnosis of toxic acute renal failure in cats. Fla. Vet. Journal. 8:14-15, 36-37.
- Panaman, R. 1981. Behavior and ecology of free-ranging female farm cats (Felis catus L.). Zeitschrift fur Tierpsychologie. 56:59-73.
- Poole, G. M. 1972. Stability of a modified live panleucopenia virus stored in liquid phase. Applied Microbiology. 24(4):663-64.
- Simberloff, D. S. 1970. Taxonomic diversity of island biotas. Evolution. 24:23-47.
- Scott, F. W., C. K. Cziza, and J. H. Gillespie. 1970. Feline viruses IV. isolation and characterization of feline panleucopenia virus in tissue culture and comparison of cytopathogenicity with feline piornavirus, herpesvirus and pathoreovirus, Cornell Vet. 60:165-183.
- Scott, P. P. 1972. The cat. In: The U.S.A.W. Handbook on care and management of laboratory animals (4th ed.). Churchill Livingston: Edinburgh and London.
- Springer, J. S. 1979. Some sources of bias and sampling error in radiotriangulation. J. Wildl. Mgmt. 43(1):926-935.
- Stonehouse, B. 1962. Ascension island and the British ornithologists' union centenary expedition 1957-59. Ibis 103 B:107-133.
- Storer, T. I. (ed.). 1962. Pacific island rate ecology. Bishop Mus. Bull. No. 225. 274 pp.
- Taylor, R. C. 1973. An atlas of Pacific island rainfall. Data Rept. No. 25. HIG-73-9.
- Taylor, R. H. 1975. What limits kiore (Rattus exulans) distribution in New Zealand. N.Z. J. Zool. 4:473-477.

Tomich, P. Q. 1970. Movement patterns of field rodents in Hawaii. Pac. Sci. 24:195-234.

Veitch, C. R. 1980. The eradication of cats from Little Barrier Island. New Zealand Wildlife Service, Department of Internal Affairs, Wellington, N. Z.

_____. 1982. Methods of eradicating feral cats from offshore islands in New Zealand. Proc. I.C.B.P. Cambridge.

Vitousek, M. J., B. Kilonsky, and W. G. Leslie. 1980. Meteorological observations in the Line Islands, 1972-1980. Data Rept. No. 38. HIG 80-7. 74 pp.

TABLE 1

ESTIMATES OF BIRD POPULATIONS OF JARVIS ISLAND

BREEDING BIRDS	1963 - 1966	1976 Nov.	1977 Oct.	1978 Oct.	1982 Jul.	1983 Nov.
Masked Booby	9000/3000	4000	950	3365	7000/3000	7000/2720
Red-footed Booby	1000/- *	-/10	-/2	-/1	500/0	850/22
Brown Booby	-/-	-/-	-/-	-/-	500/100	170/80
Red-tailed Tropicbird	-/-	-/-	-/-	-/-	-/3000	32/16
Frigatebird sp.	8000/-	-/85	-/1	-/40	1500/-	GR 400/0 LS 700/339
Sooty Tern					1,000,000/400,000	580,000/209,000
POSSIBLE BREEDING BIRDS						
Wedge-tailed Shearwater					100/-	20/-
Gray-backed Tern					10/-	2/-

Key: (Total Adults, Rounded/Breeding Pairs)

* (-/-) no data available

GR = Great frigatebird

LS = Lesser frigatebird

TABLE 1 (continued)

ESTIMATES OF BIRD POPULATIONS OF JARVIS ISLAND

NON-BREEDING BIRDS Flying/Breeding	1963 - 1966 Aug. Sep. Oct.	1976 Nov.	1977 Oct.	1978 Oct.	1982 Jul. Oct.	1983 Nov.
White-throated Storm-petrel					1/0	
Brown Noddy					1/0	1/0
Black Noddy					1/0	
Blue-gray Noddy					1/0	
White Tern					7/0	
Bristle-thighed Curlew					10/0	
Wandering Tattler					3/0	
Ruddy Turnstone					5/0	
American Golden Plover					7/0	

TABLE II

CAUSES OF MORTALITY OF
CATS ON JARVIS ISLAND

METHODS	TOTAL	HEALTHY AFTER 18 DAYS	MAX. POSSIBLE FPLV DEATH	SHOT
TRAPPED	19	10	47%	10
INOCULATED & MARKED				
INOCULATED & COLLARED	5	4	20%	4
INOCULATED & NOT MARKED	7	?	?	-
MARKED & NOT INOCULATED	2	2	0%	2
LIVE TRAPPED & SHOT	2			2
TRAPPED IN LEG-HOLD	1			1
TRAPPED IN CONIBEAR	2			2
NOT TRAPPED				
SHOT ON 14 JUNE, 1982				7
SHOT BETWEEN 27 JUNE & 10 JULY, 1982				87
SHOT BETWEEN 28 OCT. & 3 NOV., 1982				2
TOTAL	38	16	41%	117

TABLE III
BAITING AND TRAPPING SUCCESS

BAITS	TRAPNIGHT/CAPTURES	TOTAL BAITS/CONSUMED BAITS
FRESH FISH	80/11 (14%)	18/2 (11%)
CANNED CATFOOD	12/0 (0%)	
CATNIP	4/0 (0%)	
SOOTY TERN		
Prehunt	64/25 (39%)	
Posthunt	40/4 (10%)	
With CAT	200/4 (20%)	58/19 (33%)

TABLE IV
WEIGHTS OF CATS GROUPED BY COAT COLOR

[illegible]

TABLE V
SEX AND COLOR RATIOS
OF JARVIS ISLAND CATS

COLOR	MALES	FEMALES	TOTAL
<hr/>			
NUMBER			
PERCENT			
BLACK	$\frac{27}{25}$	$\frac{36}{33}$	$\frac{63}{58}$
TABBY	$\frac{14}{13}$	$\frac{17}{16}$	$\frac{31}{29}$
GRAY	$\frac{9}{8}$	$\frac{1}{0.7}$	$\frac{10}{9}$
BLACK & WHITE	$\frac{2}{1.4}$	$\frac{1}{0.7}$	$\frac{3}{3}$
COLOR?	-	$\frac{1}{1}$	$\frac{1}{1}$
TOTAL	$\frac{52}{48}$	$\frac{56}{52}$	$\frac{108}{100}$

MAJOR VEGETATION TYPES OF JARVIS ISLAND N.W.R.

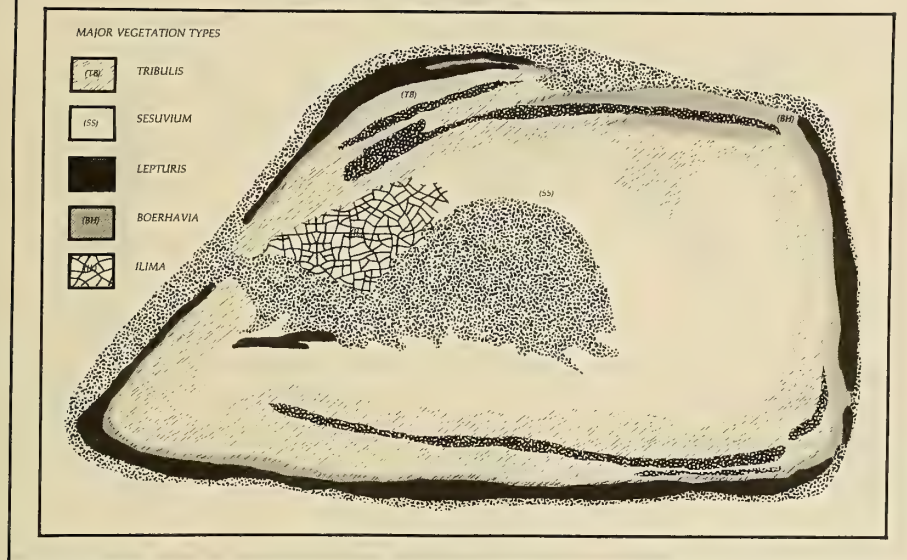


FIGURE II VEGETATION OF JARVIS ISLAND

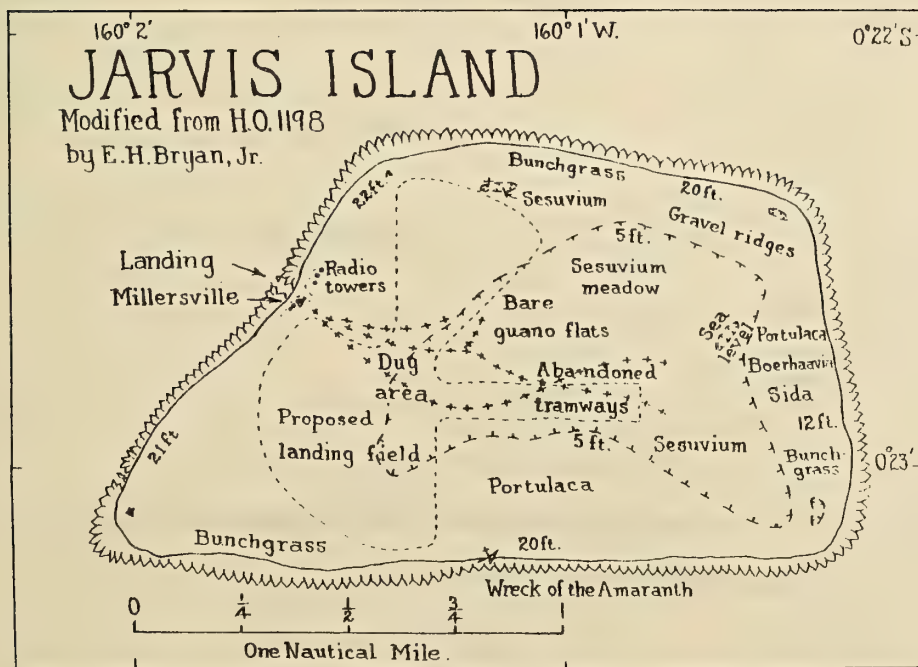


FIGURE III LANDMARKS OF JARVIS ISLAND (BRYAN 1942)

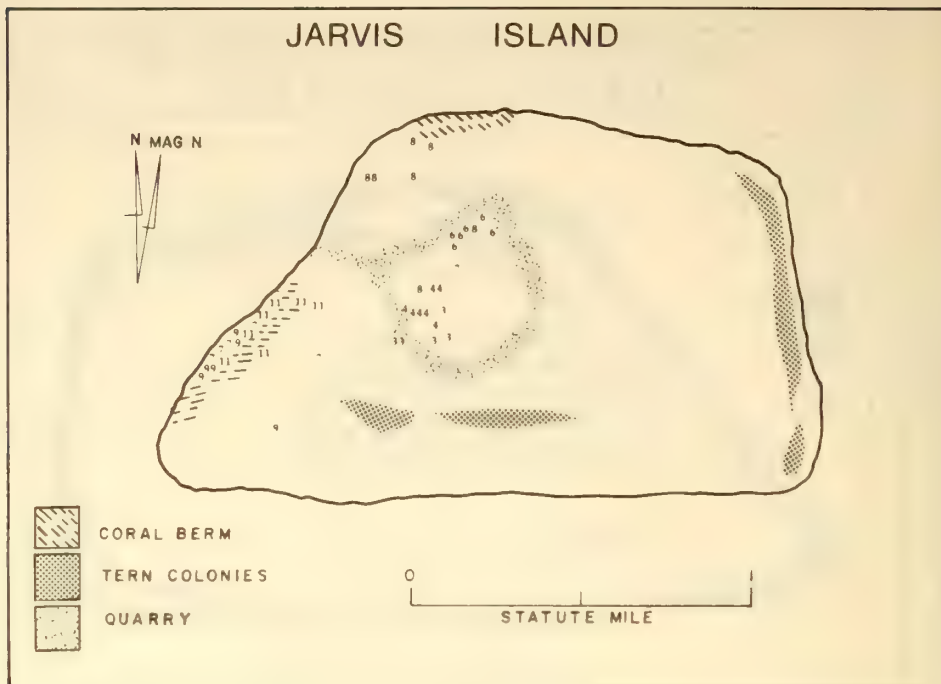


FIGURE IV

LOCATION OF COLLARED CATS DURING
RADIO-TELEMETRY FIXES

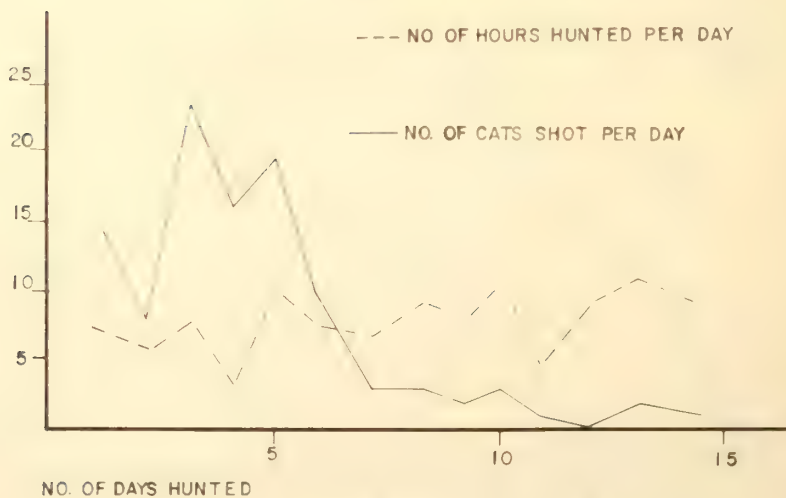


FIGURE V

AMOUNT OF TIME HUNTED
AND THE NUMBER OF CATS SHOT

VEGETATION AND FLORA
OF NUI ATOLL, TUVALU

By

C. D. WOODROFFE

ISSUED BY
THE SMITHSONIAN INSTITUTION
WASHINGTON, D. C., U.S.A.
MAY 1985

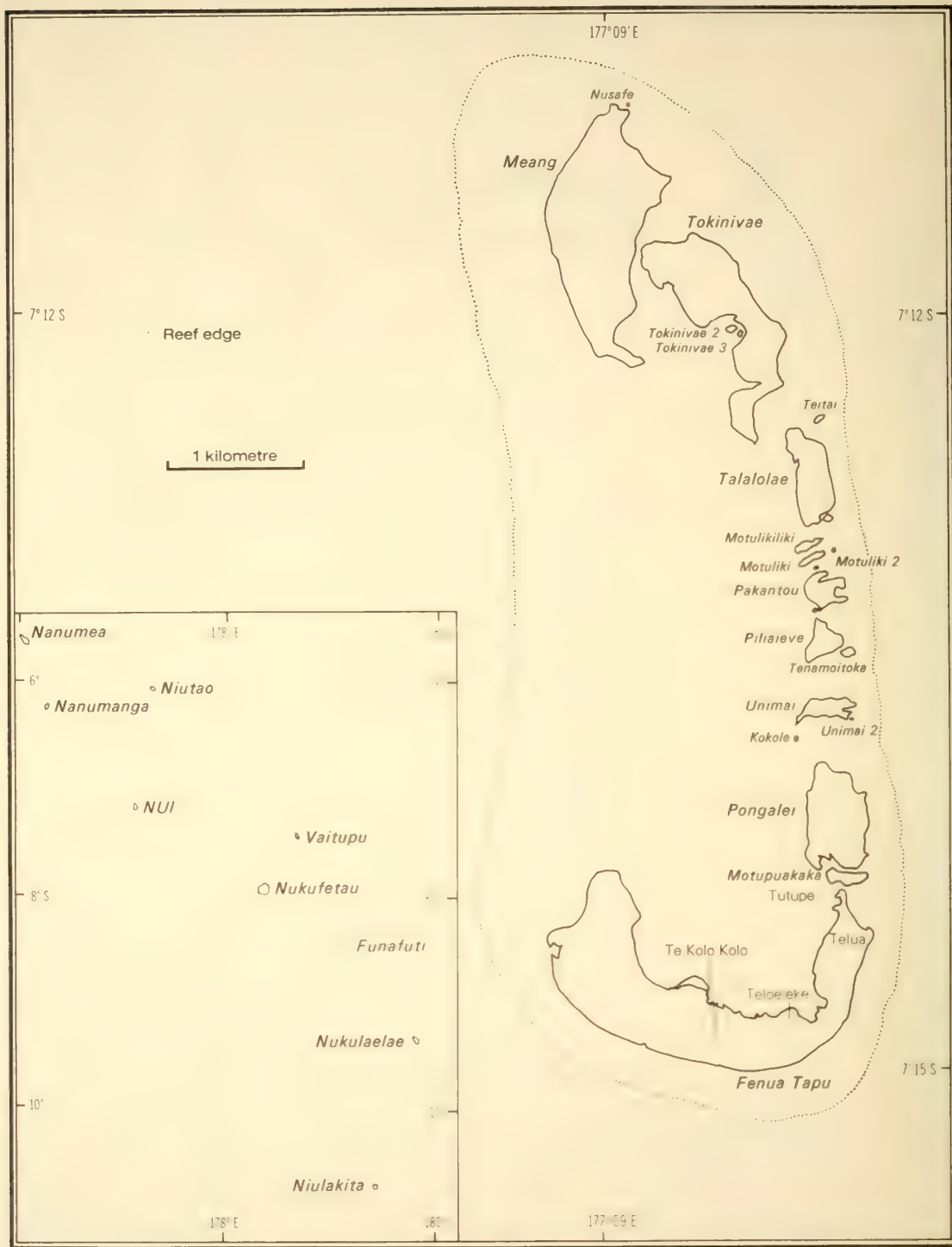


Fig. 1. Nui Atoll showing reef islands

VEGETATION AND FLORA OF NUI ATOLL, TUVALU

BY

C. D. WOODROFFE

Introduction

Tuvalu, formerly the Ellice Islands of the Gilbert and Ellice Islands until separation on 1 October 1975, is a particularly remote group of islands in the Central Pacific. There are nine islands, five of which are atolls and four reef-top islands on a reefal platform. The vegetation and flora of these islands have received little attention.

Most of the botanical collections from Tuvalu have been concentrated from the main island, Funafuti. The plants and their uses were first described by Hedley (1896). A collection of plants was made by Mrs Edgeworth David (1899) during her residence on the island in July and August 1897 as part of the Royal Society of London expedition to core the atoll. Plants were also collected by Halligan and Finckh in 1898 and their specimens and those of Mrs David were described by Maiden (1904). Since that time, the plants of Niutao have been described by Koch (1961) who has deposited a collection at the Smithsonian Institution, and those of Nanumea have been described by Chambers (1975) who has deposited a collection at the BP Bishop Museum.

Nui Atoll, to the north of the Tuvalu group, has received very little attention since it was sighted by Alvaro de Mendaña in 1568. In this paper the vegetation and flora of the atoll are described. Mapping of the vegetation of the atoll was done stereoscopically from black and white vertical aerial photographs taken in 1971 at a scale of approximately 1:10,000. Vegetation units, and where possible individual trees, were verified on the ground and the map updated during a visit to the atoll of two weeks in February 1982 and a collection of the plants was made. The specimens are deposited at the herbarium of the Department of Scientific and Industrial Research, Botany Division, Christchurch, New Zealand, and I am grateful to Dr W Sykes of the D.S.I.R. for identifications, and to Professor F R Fosberg and Dr M-H Sacht of the Smithsonian Institution for further identifications. The work was undertaken as part of a Land Resources Survey of Tuvalu, funded by F.A.O./ U.N.D.P. contracted to the Department of Geography, University of Auckland. I wish to thank Dr Roger McLean, project co-ordinator, for his guidance and encouragement, Paul Holthus and Salwa Woodroffe for help in the field and the Island Executive Officer, Lafaele, and the people of Nui for their hospitality.

Nui Atoll

Nui Atoll (lat.7°12'S long.177°10'E) lies to the north of the Tuvalu group, being approximately 130 km south of Niutao and 167 km north of Nukufetau. It consists of a reef platform approximately 7 km from north to south and 3 km from west to east (Fig. 1). There is a shallow central lagoon, and the reef islands are concentrated along the eastern rim of the atoll; the western rim being a bare reef flat, extending nearly 4 km in length. Twenty reef islands were identified and visited; these have a total surface area of 337 ha and vary from the largest, Fenua Tapu, the island on which the principal settlement is located, with an area of 138 ha, to Unimai 2 with an area of less than 0.02 ha.

The atoll is inhabited, the population in 1977 being estimated at about 650. The principal settlements are on Fenua Tapu, with a smaller temporary settlement on Meang. Other islands are visited by canoe, or by walking around the eastern reef flat at low tide.

Nui experiences a warm, humid climate throughout the year. The prevailing winds are easterlies. It receives about 3000 mm of rainfall annually with more than 200 rainy days per year.

The reef islands of Nui are generally sandy with varying amounts of humus incorporated into the sand. A cemented rubble conglomerate platform underlies many of the islands and is prominent on the eastern rim of the atoll and along much of the lagoonward shore. The only extensive coral shingle or rubble ridges occur to the northwest of Meang.

Nui is interesting in that the people of Nui show a much closer relationship to the islands of Micronesia than do other Tuvaluans, despite there being three islands closer to Kiribati (Gilbert Is.). Tradition has it that early Samoan settlers on Nui were largely replaced by people from Tabiteuea and Beru in Kiribati. The language on Nui is much more closely related to the language of Kiribati than on other islands in Tuvalu and names for things, including plants, are often different from the names used in the rest of Tuvalu. For instance, the root crop Cyrtosperma is called 'babai' on Nui whereas it is 'pulaka' on the other islands of Tuvalu. Where it has been possible to establish local Nui names for plants these are reported below.

Vegetation Units

The flora of Nui consists of at least 86 species. The largest number of species occurs on Fenua Tapu; 83 species were observed, many of which were crops or ornamentals found around the village. The following distinct vegetation units could be recognised:

Pemphis scrub

Pemphis acidula forms dense thickets at several sites, particularly on the lagoonward shore, on Nui Atoll. Pemphis occurs either on the dissected conglomerate platforms of the reef islands, or on a substrate of

medium angular coral rubble or coarse sand, where inundation is infrequent and there is a sporadic cover of desiccated algal nodules or an algal mat.

Pemphis scrub is found on the dissected conglomerate platform along the lagoonward shore of Fenua Tapu where it is 4-5m tall and forms either a continuous fringe less than 30m wide along the coast, or a discontinuous fringe scarcely more than an individual shrub wide. Similar Pemphis scrub occurs on a rubble or sand substrate near Telaeleke on Fenua Tapu, and at the northeastern end of that island, on Tokinivae, Pongalei and Talalolae. Within the Pemphis scrub, individual shrubs are spaced 4-5m apart, becoming increasingly sparse in the island interiors. On Tokinivae Pemphis may reach 10m tall; on Pongalei 8-10m tall, and on Talalolae and Fenua Tapu it rarely exceeds 6m tall.

Pemphis scrub on the lagoonward shores grows so densely that there are generally no other plants associated with it, except occasionally the fern Polypodium. However on Tokinivae, Pongalei and Talalolae sparser Pemphis scrub extends inland, over a substrate of fine coral rubble and pinkish sand with an algal mat veneer, or more usually a cover of small black algal nodules, and in these areas Pemphis is generally less than 2m tall and Tournefortia and Scaevola also occur with a ground vegetation of Fimbristylis, Lepturus and Cassytha.

A scrub composed of Pemphis is a common element of the vegetation of islands in the Pacific. It forms a distinct coastal zone on the atolls of the Cook Islands (Linton, 1933; Stoddart, 1975), the Tokelau Islands (Parham, 1971), and continues north through Kiribati (Luomala, 1953; Moul, 1957), and the Marshalls and Marianas (Fosberg, 1960). On Nui Atoll Pemphis scrub occurs on the lagoonward side of many of the reef islands where these are narrowest, and extends into the islands reaching towards the oceanward shore. Pemphis tends to be growing at a lower elevation than surrounding vegetation, where it is prone to occasional flooding, and the areas of Pemphis scrub probably represent old infilled inter-island channels. The area at Telaeleke on Fenua Tapu has Pemphis scrub reaching to within 30m of the oceanward shore separated from the sea by a sand ridge.

Scaevola scrub

A dense scrub of Scaevola sericea occurs as a fringe around most of the perimeter of the majority of the reef islands of Nui, and often extends inland, generally in association with Acalypha, beneath Coconut woodland. The fringe may develop on sandy or on coral rubble substrates. It is particularly well developed along the oceanward shore of the reef islands, where it characteristically forms a fringe 15-20cm wide, rarely exceeding 4m tall, landward of which Coconut woodland is found with the outermost coconuts overhanging the Scaevola.

At the northeast of Fenua Tapu Scaevola scrub forms a belt approximately 20m wide on a beach ridge of fine coral rubble and sand. This is a recently formed ridge which links what was previously the island of Tutupe to Telua, Fenua Tapu.

Over much of the atoll Scaevola scrub is monospecific and the dense fleshy branches of Scaevola make the scrub penetrable only with difficulty. The creepers Canavalia and Cassytha where they occur on the scrub also impede passage. In some places Tournefortia, Cordia, Pandanus or Guettarda may be emergent while Triumfetta occurs on the ground.

In addition to the coastal Scaevola scrub, Scaevola is also an important element of the inland scrub vegetation. A sparse Scaevola scrub, consisting of shrubs of Scaevola rarely exceeding 3m tall and emergent Pandanus, occurs on a series of north-south ridges of fine angular coral rubble to the northwest of Meang. A patchy ground cover of Boerhavia, Fimbristylis, Nephrolepis and Polypodium is found, and much of the vegetation is shrouded in Cassytha. Towards the interior of Meang, Tournefortia, Acalypha, Guettarda and Pisonia become more important and the sparse Scaevola scrub gives way to Scaevola/Acalypha scrub.

Much of the interior of reef islands on Nui has a scrub vegetation composed principally of Scaevola sericea and Acalypha amentacea var. On Fenua Tapu Scaevola is the main element of the scrub, 3-4m tall, with Pipturus, Ficus, Guettarda, Morinda, Nephrolepis, Polypodium and Fimbristylis present and Acalypha only locally important. Elsewhere, as on Pongalei, Acalypha is the most conspicuous element of the scrub and Tournefortia, Asplenium and Boerhavia are also common.

Pandanus is an important component throughout this vegetation unit. It is infrequent in most of the scrubland of Fenua Tapu, though becoming more common in the Scaevola/Acalypha scrub to the eastern end of the island. On Pongalei Pandanus is abundant within the Scaevola/Acalypha scrub and on Meang it is extremely common. These scrub areas are important for the collection of Pandanus leaves, and the general increase in occurrence of Pandanus with distance from the village may reflect decreasing collection intensity.

The Scaevola/Acalypha scrub is also found beneath Coconut woodland and beneath Pisonia woodland. Scaevola, and to a lesser extent Acalypha, grows best where there is plenty of light and is not well developed under dense woodland. Scrub is particularly important in areas of young Pisonia under trees up to 16m tall.

Scaevola scrub forms a seaward belt on other islands in Tuvalu and has been described from Funafuti (Hedley, 1896) and over much of Nanumea (Chambers, 1975). It forms a prominent beach crest facies in the Tokelau Islands (Parham, 1971) on Swains Island (Whistler, 1983), and on Onotoa, Kiribati (Moul, 1957) and is one of the most consistent vegetation units throughout Pacific atolls (Fosberg, 1953).

Tournefortia scrub

Tournefortia argentea is generally taller than, and forms a more penetrable scrub than Scaevola. Small stands of Tournefortia occur within Scaevola scrub, and larger stands form a distinct scrub unit at the northern and southern ends of Pongalei, at the western end and to the southwest of Tokinivae and at the head of inlets on the ocean side of Pakantou and Unimai.

The most extensive fringe of Tournefortia scrub however occurs along the sandy beach crest of the western shore of Meang. Here the scrub is 15-25m wide, and reaches 6-8m tall. Scaevola is found within the unit, and stands of Scaevola and Tournefortia alternate along the coast of central Meang, with replacement of Tournefortia by Scaevola scrub on the coarser substrate to the north of Meang. The Tournefortia scrub is much more open than Scaevola scrub and individual trees are spaced 6-8m apart. Canavalia, Triumfetta and Boerhavia occur within the scrub, while coconut, Guettarda and Pandanus are occasionally emergent.

Small pockets of Tournefortia scrub also occur inland. These are rarely extensive and consist of only one or a few individuals up to 17m tall. The vegetation within these pockets is usually typical Scaevola/Acalypha scrub or Pipturus/Acalypha/Scaevola scrub, sometimes with Pisonia. Similar Tournefortia scrub is an important littoral vegetation of many atolls in the Pacific, including the Tokelau Islands, Marshall Islands, Caroline Islands and northern Cook Islands (Linton, 1933; Fosberg, 1960; Niering, 1961; Parham, 1971).

Pipturus/Acalypha/Scaevola scrub

Pipturus/Acalypha/Scaevola scrub is an inland scrub similar to the Scaevola/Acalypha scrub, but may be distinguished by the dominance of Pipturus argenteus in the upper storey. Pipturus grows to 10m or more tall, and often has several trees of Tournefortia in association, and occasionally Pisonia also. The lighter colour of the canopy of these emergent species allows recognition of this unit on aerial photographs. The lower storey vegetation is usually species-rich, with Scaevola, Acalypha, Ficus, Guettarda, Pandanus and the ferns Polypodium, Asplenium, Nephrolepis and Pteris. Pipturus/Acalypha/Scaevola scrub is found on Motupuakaka, Talalolae and Tokinivae, and to a lesser extent on Fenua Tapu.

Rhizophora scrub

Rhizophora stylosa is not extensive on Nui and is found only on the lagoonward shore of Fenua Tapu at Telaeleke. Here it rarely exceeds 4m in height, and forms a fringe around the edge of the conglomerate platform. This fringe is often only one tree wide, exceptionally reaching a belt 40m wide. Rhizophora scrub is monospecific and is backed by Pemphis scrub. Rhizophora and Pemphis may be interspersed where the two units are juxtaposed. Rhizophora scrub on Nui is more open than that described from a basin on Vaitupu (Woodroffe and Moss, 1984). Cracks and fissures in the surface of the reef flat in this mangrove area were observed to flood and drain the area with the tides.

Lumnitzera scrub

The red-flowered mangrove Lumnitzera littorea occurs in two isolated pockets, each less than 20m x 30m wide, in the Pemphis scrub area of Telaeleke, Fenua Tapu. Lumnitzera reaches 3.5-4.5m tall, and each pocket is surrounded by Pemphis which is the only species recorded in association with Lumnitzera.

Morinda thicket

A thicket, dominated by Morinda citrifolia, occurs at one location surrounding a muddy depression to the east of Pongalei. The stand is only about 10m x 25m wide and is composed of Morinda 8m tall, spaced approximately 5m between individuals. The only associated plants are Ficus and the fern Asplenium.

Pandanus grove

Small groves of Pandanus tectorius occur around the coast of the reef islands of Nui, but do not form Pandanus woodland like that recorded on atolls, such as Aitutaki and Palmerston, in the Cook Islands (Stoddart, 1975; Sykes, 1976), or Kayangel in the Palau Islands (Gressitt, 1952). The groves are generally composed of 5-10 individuals which are 8-10m tall, though Pandanus on Fenua Tapu can reach as much as 18m tall.

Coconut woodland

The most important woodland type on Nui is dominated by the coconut Cocos nucifera. The coconut palms exhibit a great variation in height and density, reaching 26m in some places. In those areas, as around the principal settlement, where there is regular collection of drinking nuts, the woodland is kept relatively clear of undergrowth while elsewhere it may be unattended and entirely overgrown with scrub. Such scrub tends to be dominated by either Scaevola or Acalypha, with Pandanus, Nephrolepis, Morinda, Guettarda, Ficus and Polypodium. Elsewhere Pisonia and Asplenium occur within the coconut woodland, or Asplenium alone may form a dense carpet between the palms.

Pisonia woodland

Woodland of Pisonia grandis is the most extensive natural woodland on Nui and occurs over much of the interior of the various reef islands, occasionally being exposed on the coast. It is well developed even on some of the smaller islands such as Teitai and Tenamoitoka.

The most impressive stands of Pisonia woodland occur on Unimai, southern Meang and on Fenua Tapu at Te Kolokolo and near Telaeleke, in the latter two instances in association with deposits of phosphate. The massive Pisonia of Unimai reach heights of 22-24m and the woodland is dominated by immense individuals which exceed 1m in diameter of the trunk. Acalypha is prominent in the understory, with Ficus and rare Guettarda and Pandanus. The fern Asplenium, of which the young fronds are eaten as a spinach, is also an important associate in Pisonia woodland occurring both epiphytically on the Pisonia trees and on the coral rubble and sand substrate. On Meang similar massive Pisonia trees occur more sparsely, giving the woodland a more open appearance. In addition other large trees, including Hernandia, Calophyllum and occasional breadfruit Artocarpus are found in the woodland; the understory vegetation is dominated by Asplenium but also contains Acalypha, Ficus and Polypodium.

The Pisonia woodland at Te Kolokolo and Telaeleke on Fenua Tapu is also composed of large individual trees, many up to 20m tall; again Ficus, Morinda and Acalypha are important. The ferns Nephrolepis and Polypodium are found on the ground, however Asplenium is less abundant perhaps because the site is closer to the village. The Te Kolokolo area in particular has been altered as a result of felling of Pisonia trees, though the ability of Pisonia to shoot up from fallen limbs means that there has also been some regrowth.

Elsewhere stands of Pisonia woodland are composed of less massive individuals often exceeding 18m in height but rarely more than 50cm diameter, and coconuts are more frequent. Such a Pisonia woodland is a typical woodland of many atolls in the Pacific including Kiribati, the Tokelau Islands, Cook Islands and Caroline Islands (Moul, 1957; Parham, 1971; Stoddart, 1975; Marshall, 1975), and is frequently associated with phosphatic substrates (Fosberg, 1953).

Hernandia woodland

Woodland dominated by Hernandia sonora occurs at several sites just east of the pig wall on Fenua Tapu. Here large individual trees of Hernandia reaching 18m tall dominate small stands of woodland. Occasionally Pisonia may be present, and towards the north coast of Fenua Tapu Cordia is also associated with the Hernandia woodland. In view of the use of timber of Hernandia and its speed of growth, these groves of Hernandia located close to the village, and the individual trees in and around the village, have probably been planted. In a stand of Hernandia woodland on the central road of Fenua Tapu Acalypha is abundant, and Ficus, Guettarda and Asplenium are all frequent. Present but less common are Pipturus, Nephrolepis and Polypodium.

Hernandia woodland also occurs extensively on Meang, though over much of southeastern Meang Hernandia and Pisonia grow in association forming a mixed open woodland more than 20m tall. Hernandia and Pisonia are closely associated in forests on Nanumea (Chambers, 1975) and have also been described together on Swains Island (Whistler, 1983) and on Aitutaki and Palmerston in the Cook Islands (Stoddart, 1975; Sykes, 1976).

Pulaka pits

Small pits of pulaka Cyrtosperma chamissonis (locally called Babai) occur on a number of islands (Small, 1972). One is found on Piliaieve, and several, less than 10m in diameter, occur on Tokinivae. The most pits, and those most important for production of pulaka, presently occur around the village on northwestern Fenua Tapu. Here pit construction is still underway and pits are regularly cultivated. In addition to pulaka, there is talo Colocasia, and banana Musa; there are also several common weeds, most notably Ludwigia, Cyperus and Alternanthera.

A further pulaka pit occurs on Meang. This is presently largely abandoned and pulaka grows only around the edge and in smaller secondary pits. Most of the pulaka pit is covered with Paspalum distichum with patches of Cyperus. Scaevola is found around the pit and grows with Ficus, Guettarda and Polypodium on small islands in the pit.

Village and Gardens

Natural vegetation has been almost totally replaced in the areas in which population is concentrated. The village is dominated by useful trees, particularly by the breadfruit Artocarpus, drinking coconuts, as well as scattered Hernandia trees. Additional areas, such as the hospital, guest house, and cemeteries have largely been planted with ornamental species, and these areas also support several weedy species. Ornamental garden plants include Pseuderanthemum atropurpureum, Clerodendrum inerme, Polyscias guilfoylei, Lantana camara, Plumeria rubra, Gardenia taitensis, Acalypha wilkesiana and Mirabilis jalapa.

The flora

The vascular plants collected or sighted on Nui Atoll are listed below. Numbers refer to voucher specimens deposited at the DSIR, Christchurch.

ASPLENIACEAE

Asplenium nidus L.

[local name - laukatapa]

Fenua Tapu: Woodroffe 189; Motupuakaka: sight; Pongalei: sight; Kokole: sight; Unimai: sight; Tenamoitoka: sight; Piliaieve: sight; Motuliki: sight; Motuliki 2: sight; Motulikiliki: sight; Talalolae: sight; Teitai: sight; Tokinivae: sight; Meang: sight; Nusafe: sight.

DAVALLIACEAE

Nephrolepis acutifolia (Desv.) Christ.

[local name - lautamatama]

Fenua Tapu: Woodroffe 140, 188; Motupuakaka: sight; Pongalei: sight; Kokole: sight; Unimai: sight; Tenamoitoka: sight; Piliaieve: sight; Pakantou: sight; Sikaiana: sight; Motuliki: sight; Motulikiliki: sight; Talalolae: sight; Teitai: sight; Tokinivae: sight; Meang: sight; Tokinivae 2: sight.

Nephrolepis saligna Cass.

[local name - lautamatama]

Fenua Tapu: Woodroffe 187

POLYPODIACEAE

Polypodium scolopendria Burm.f.

[local name - maile]

Fenua Tapu: Woodroffe 120; Motupuakaka: sight; Pongalei: sight; Unimai: sight; Unimai 2: sight; Tenamoitoka: sight; Piliaieve: sight; Pakantou: sight; Sikaiana: sight; Motuliki: sight; Motuliki 2: sight; Motulikiliki: sight; Talalolae: sight; Teitai: sight; Tokinivae: sight; Meang: sight; Tokinivae 2: sight.

PSILOTACEAE

Psilotum nudum (L.) Beauv.

Fenua Tapu: Woodroffe 112

PTERIDACEAE

Pteris tripartita Sw.

[local name - te laukimoa]

Fenua Tapu: Woodroffe 119; Unimai: sight; Meang: sight.

PANDANACEAE

Pandanus tectorius Park. (s.l.)

[local names - teou, teto]

Fenua Tapu: sight; Motupuakaka: sight; Pongalei: sight; Kokole: sight; Unimai: sight; Unimai 2: sight; Tenamoitoka: sight; Piliaieve: sight; Pakantou: sight; Sikaiana: sight; Motuliki: sight; Motuliki 2: sight; Motulikiliki: sight; Talalolae: sight; Teitai: sight; Tokinivae: sight; Meang: sight; Nusafe: sight; Tokinivae 2: sight; Tokinivae 3: sight.

CYCADACEAE

Cycas circinalis L.Fenua Tapu: Woodroffe 185

GRAMINEAE

Bambusa sp.Fenua Tapu: Woodroffe 168Cenchrus echinatus L.Fenua Tapu: Woodroffe 113, 196Digitaria pacifica StapfFenua Tapu: Woodroffe 127Eleusine indica (L.) Gaertn.Fenua Tapu: Woodroffe 103, 124Eragrostis tenella (L.) P.Beauv.ex Roem. & Schult.Fenua Tapu: Woodroffe 110; Piliaieve: sight.Lepturus repens (Forst.f) R.Br.

Fenua Tapu: sight; Motupuakaka: sight; Pongalei: sight; Kokole: sight; Unimai: sight; Unimai 2: sight; Tenamoitoka: sight; Piliaieve: sight; Pakantou: sight; Sikaiana: Woodroffe 131; Motuliki: sight; Motulikiliki: sight; Talalolae: Woodroffe 180, 181, 182; Tokinivae: sight; Meang: sight; Nusafe: sight; Tokinivae 2: sight; Tokinivae 3: sight.

Paspalum distichum L.Fenua Tapu: Woodroffe 147; Meang: sightSaccharum officinarum L.

Fenua Tapu: sight.

Stenotaphrum micranthum (Desv.) C.E.Hubb.

Fenua Tapu: sight; Motupuakaka: sight; Pongalei: sight;
Tenamoitoka: sight; Pakantou: sight; Motulikiliki: sight;
Talalolae: Woodroffe 179; Tokinivae: sight; Meang: sight.

Thuarea involuta (Forst.f.) R.Br.

Fenua Tapu: Woodroffe 109

CYPERACEAE

Cyperus alternifolius L.

Fenua Tapu: sight; Meang: sight

Fimbristylis cymosa R.Br.

Fenua Tapu: Woodroffe 111, 194; Motupuakaka: sight; Pongalei: sight;
Unimai: sight; Piliaieve: sight; Pakantou: sight; Tokinivae: sight;
Meang: sight; Tokinivae 2: sight

PALMAE

Cocos nucifera L.

[local name - Niu]

Fenua Tapu: sight; Motupuakaka: sight; Pongalei: sight; Kokole:
sight; Unimai: sight; Unimai 2: sight; Tenamoitoka: sight; Piliaieve:
sight; Pakantou: sight; Sikaiana: sight; Motuliki: sight; Motuliki 2:
sight; Motulikiliki: sight; Talalolae: sight; Teitai: sight;
Tokinivae: sight; Meang: sight; Nusafe: sight; Tokinivae 2: sight;
Tokinivae 3: sight.

ARACEAE

Colocasia esculenta (L.) Schott

[local name - talo]

Fenua Tapu: sight; Tokinivae: sight; Meang: sight

Cyrtosperma chamissonis (Schott) Merr.

[local name - babai]

Fenua Tapu: sight; Piliaieve: sight; Tokinivae: sight; Meang:
sight.

AMARYLLIDACEAE

Crinum asiaticum L.

[local name - te luhe]

Fenua Tapu: Woodroffe 135

TACCACEAE

Tacca leontopetaloides (L.) O.Ktze.

[local name - masua]

Fenua Tapu: Woodroffe 115

MUSACEAE

Musa sp.

[local name - ulu]

Fenua Tapu: sight; Meang: sight.

CASUARINACEAE

Casuarina equisetifolia L.Fenua Tapu: Woodroffe 171

MORACEAE

Artocarpus altilis (Park.) Fosb.

[local name - mei]

Fenua Tapu: Woodroffe 193; Pongalei: sight; Tokinivae: sight; Meang: sight.Ficus prolixa Forst. f.Fenua Tapu: Woodroffe 122Ficus tinctoria Forst.f.

[local name - pelo]

Fenua Tapu: Woodroffe 139; Motupuakaka: sight; Pongalei: sight; Unimai: sight; Tenamoitoka: sight; Piliaieve: sight; Pakantou: sight; Motuliki: sight; Motuliki 2: sight; Motulikiliki: sight; Talalolae: sight; Teitai: sight; Tokinivae: sight; Meang: sight; Nusafe: sight; Tokinivae 2: sight; Tokinivae 3: sight.

URTICACEAE

Laportea interrupta (L.) ChewFenua Tapu: Woodroffe 195; Pongalei: Woodroffe 133; Tokinivae: sight; Meang: sightPilea microphylla (L.) Lieb.Fenua Tapu: Woodroffe 186Pipturus argenteus (Forst.f.) Wedd.

[local name - te paul]

Fenua Tapu: Woodroffe 136; Motupuakaka: sight; Pongalei: sight; Unimai: sight; Tenamoitoka: sight; Piliaieve: sight; Pakantou: sight; Motuliki: sight; Motulikiliki: sight; Talalolae: sight; Teitai: sight; Tokinivae: sight; Meang: sight; Nusafe: sight; Tokinivae 2: sight; Tokinivae 3: sight.

OLACACEAE

Ximenia americana L.

[local name - kanana]

Fenua Tapu: Woodroffe 129; Motupuakaka: sight; Pongalei: sight; Unimai: sight; Tenamoitoka: sight; Piliaieve: sight; Pakantou: sight; Talalolae: sight; Tokinivae: Woodroffe 161; Meang: Woodroffe 157

AMARANTHACEAE

Achyranthes aspera L. approaching velutina H&A, [local name - sisi vao]Fenua Tapu: Woodroffe 126; Motupuakaka: sight; Tokinivae: sight; Meang: sight.Alternanthera sessilis (L.) R.Br.Fenua Tapu: Woodroffe 150

NYCTAGINACEAE

Boerhavia tetrandra Forst.

Fenua Tapu: Woodroffe 104, 130; Motupuakaka: sight; Pongalei: sight; Piliaieve: sight; Pakantou: sight; Sikaiana: sight; Motuliki: sight; Motulikiliki: sight; Talalolae: sight; Tokinivae: sight; Meang: sight; Tokinivae 2: sight; Tokinivae 3: sight.

Mirabilis jalapa L.

[local name - petel]

Fenua Tapu: Woodroffe 172

Pisonia grandis R.Br.

[local name - puka vai]

Fenua Tapu: sight; Motupuakaka: sight; Pongalei: sight; Unimai: sight; Tenamoitoka: sight; Piliaieve: sight; Pakantou: sight; Motuliki: sight; Motuliki 2: sight; Motulikiliki: sight; Talalolae: sight; Teitai: sight; Tokinivae: Woodroffe 163; Meang: sight; Nusafe: sight.

PORTULACACEAE

Portulaca australis Endl..

Fenua Tapu: Woodroffe 197

Portulaca lutea Sol. or P.oleracea L.

Piliaieve: Woodroffe 101; Pakantou: sight; Tokinivae: sight; Meang: sight

LAURACEAE

Cassytha filiformis L.

[local name - te louku]

Fenua Tapu: sight; Motupuakaka: sight; Pongalei: sight; Unimai: sight; Piliaieve: sight; Pakantou: sight; Sikaiana: sight; Motuliki: sight; Motulikiliki: sight; Talalolae: Woodroffe 178; Tokinivae: sight; Meang: sight; Tokinivae 2: sight.

HERNANDIACEAE

Hernandia sonora L.

[local name - puka]

Fenua Tapu: Woodroffe 118; Pongalei: sight; Talalolae: sight; Tokinivae: sight; Meang: sight

CRASSULACEAE

Bryophyllum pinnatum (Lam.) Kurz (= Kalanchoe pinnata (Lam.) Pers.)

Fenua Tapu: Woodroffe 138

LEGUMINOSAE

Canavalia cathartica Thou.

[local name - lokou]

Fenua Tapu: sight; Motupuakaka: sight; Pongalei: sight; Kokole: sight; Unimai: sight; Unimai 2: sight; Tenamoitoka: sight; Piliaieve: sight; Pakantou: sight; Motuliki: sight; Talalolae: sight; Tokinivae: Woodroffe 162; Meang: sight; Nusafe: sight; Tokinivae 2: sight.

Vigna marina (Burm.) Merr.

[local name - te louku]

Fenua Tapu: Woodroffe 107; Pongalei: sight; Unimai: sight.

SURIANACEAE

Suriana maritima L.

[local name - ngie]

Motupuakaka: Woodroffe 128; Pongalei: sight; Tokinivae: sight.

EUPHORBIACEAE

Acalypha amentacea Roxb. var.

[local name - kakarapus]

Fenua Tapu: Woodroffe 137; Motupuakaka: sight; Pongalei: sight; Unimai: sight; Tenamoitoka: sight; Piliaieve: sight; Pakantou: sight; Motuliki: sight; Talalolae: sight; Tokinivae: sight; Meang: sight; Tokinivae 2: sight; Tokinivae 3: sight.

Acalypha amentacea ssp. wilkesiana (Muell.-Arg.) Fosb.

Fenua Tapu: Woodroffe 169

Euphorbia chamissonis (Kl. & Gke) Boiss.

Fenua Tapu: Woodroffe 134; Motupuakaka: sight; Pongalei: sight.

Jatropha curcas L.

Fenua Tapu: Woodroffe 184

Phyllanthus amarus Schum.

[local name - te uteute]

Fenua Tapu: Woodroffe 105

TILIACEAE

Triumfetta procumbens Forst. f.

[local name - kiaou]

Fenua Tapu: Woodroffe 154; Motupuakaka: sight; Pongalei: sight; Kokole: sight; Tenamoitoka: sight; Piliaieve: sight; Pakantou: sight; Talalolae: sight; Meang: sight.

MALVACEAE

Sida fallax Walp.

Fenua Tapu: Woodroffe 164; Tokinivae: sight

GUTTIFERAE

Calophyllum inophyllum L.

[local name - itai]

Fenua Tapu: Woodroffe 176; Motupuakaka: sight; Pongalei: sight; Unimai: sight; Tenamoitoka: sight; Piliaieve: sight; Pakantou: sight; Talalolae: sight; Teitai: sight; Tokinivae: sight; Meang: sight.

CARICACEAE

Carica papaya L.

[local name - esi]

Fenua Tapu: Woodroffe 191

CUCURBITACEAE

Cucurbita pepo L.Fenua Tapu: Woodroffe 190

LYTHRACEAE

Pemphis acidula Forst.

[local name - ngie]

Fenua Tapu: sight; Pongalei: sight; Unimai: sight; Piliaieve: sight; Pakantou: sight; Motuliki: sight; Talalolae: sight; Tokinivae: Woodroffe 160; Meang: sight; Tokinivae 2: sight.

LECYTHIDACEAE

Barringtonia asiatica L.

[local name - ulu]

Fenua Tapu: Woodroffe 175; Pongalei: sight; Pakantou: sight; Talalolae: sight; Tokinivae: sight; Meang: sight.

RHIZOPHORACEAE

Rhizophora stylosa Griff.

[local name - te tongo]

Fenua Tapu: Woodroffe 146

COMBRETACEAE

Lumnitzera littorea (Jack) Voigt

[local name - tangali]

Fenua Tapu: Woodroffe 116Terminalia samoensis Rech.

[local name - te ipe]

Fenua Tapu: sight; Motupuakaka: sight; Pongalei: sight; Unimai: sight; Unimai 2: sight; Piliaieve: sight; Pakantou: sight; Motuliki: sight; Motuliki 2: sight; Motulikiliki: sight; Teitai: sight; Tokinivae: sight; Meang: Woodroffe 155

ONAGRACEAE

Ludwigia octovalvis (Jacq.) RavenFenua Tapu: Woodroffe 148

CONVOLVULACEAE

Ipomoea batatas (L.) Lam.Fenua Tapu: Woodroffe 192Ipomoea macrantha R. & S.Talalolae: Woodroffe 177; Meang: sight

BORAGINACEAE

Cordia subcordata Lam.

[local name - kanava]

Fenua Tapu: Woodroffe 152; Pongalei: sight; Unimai: sight; Piliaieve: sight; Pakantou: sight; Motuliki: sight; Motulikiliki: sight; Talalolae: sight; Teitai: sight; Tokinivae: sight; Meang: sight; Tokinivae 2: sight

Tournefortia argentea L.f (= Messerschmidia argentea (L.f.) Johnst.
= Argusia argentea (L.f.) Heine)

[local name - tausunu]

Fenua Tapu: Woodroffe 165; Motupuakaka: sight; Pongalei: sight;
Unimai: sight; Piliaieve: sight; Pakantou: sight; Motuliki: sight;
Motulikiliki: sight; Talalolae: sight; Teitai: sight; Tokinivae: sight;
Meang: sight; Nusafe: sight; Tokinivae 2: sight; Tokinivae 3: sight.

VERBENACEAE

Clerodendrum inerme (L.) Gaertn,

[local name - inato]

Fenua Tapu: Woodroffe 167

Lantana camara L.

[local name - kai puaka]

Fenua Tapu: Woodroffe 166

Premna obtusifolia R.Br.

[local name - te anga]

Fenua Tapu: Woodroffe 153; Pongalei: sight.

SOLANACEAE

Physalis angulata L.

[local name - te peen]

Fenua Tapu: Woodroffe 145

Solanum lycopersicum L. (= Lycopersicon esculentum Mill.)

Fenua Tapu: Woodroffe 183

ACANTHACEAE

Pseuderanthemum carruthersii var. atropurpureum (Bull) Fosb.

Fenua Tapu: Woodroffe 159

RUBIACEAE

Gardenia taitensis DC.

[local name - siale]

Fenua Tapu: Woodroffe 174

Guettarda speciosa L.

[local name - uli]

Fenua Tapu: Woodroffe 121; Motupuakaka: sight; Pongalei: sight;
Kokole: sight; Unimai: sight; Unimai 2: sight; Tenamoitoka: sight;
Pakantou: sight; Sikaiana: sight; Motuliki: sight; Motuliki 2: sight;
Motulikiliki: sight; Talalolae: sight; Teitai: sight; Tokinivae: sight;
Meang: sight; Nusafe: sight; Tokinivae 2: sight; Tokinivae 3: sight.

Hedyotis romanzoffiensis (Cham. & Schlecht Fosb.

Pakantou: Woodroffe 132; Talalolae: sight; Tokinivae: sight;
Meang: Woodroffe 156 (Western extension for species)

Morinda citrifolia L.

[local name - te non]

Fenua Tapu: Woodroffe 143; Motupuakaka: sight; Pongalei: sight; Kokole: sight; Unimai: sight; Tenamoitoka: sight; Piliaieve: sight; Pakantou: sight; Sikaiana: sight; Motuliki: sight; Motulikiliki: sight; Talalolae: sight; Teitai: sight; Tokinivae: sight; Meang: sight; Tokinivae 2: sight,

APOCYNACEAE

Neisosperma oppositifolia (Lam.) Fosb. & Sachet [local name - pau pau]

Fenua Tapu: Woodroffe 125; Pongalei: sight; Unimai: sight; Tenamoitoka: sight; Meang: sight.

Plumeria rubra L.

[local name - pua fiti]

Fenua Tapu: Woodroffe 170

ARALIACEAE

Polyscias guilfoylei (Bull) Bailey

Fenua Tapu: Woodroffe 142, 173

GOODENIACEAE

Scaevola sericea Vahl (= S. taecada (Gaertn.) Roxb.) [local name - ngahu]

Fenua Tapu: Woodroffe 158; Motupuakaka: sight; Pongalei: sight; Kokole: sight; Unimai: sight; Unimai 2: sight; Tenamoitoka: sight; Piliaieve: sight; Pakantou: sight; Sikaiana: sight; Motuliki: sight; Motuliki 2: sight; Motulikiliki: sight; Talalolae: sight; Teitai: sight; Tokinivae: sight; Meang: sight; Nusafe: sight; Tokinivae 2: sight; Tokinivae 3: sight.

COMPOSITAE

Adenostemma lanceolatum Miq.

Fenua Tapu: Woodroffe 117

Eclipta prostrata (L.) L.

Fenua Tapu: Woodroffe 114

Synedrella nodiflora (L.) Gaertn.

Fenua Tapu: Woodroffe 123

Vernonia cinerea (L.) Less.

Fenua Tapu: Woodroffe 106

Wollastonia biflora (L.) DC.

[local name - louku]

Fenua Tapu: Woodroffe 108

Discussion

The vegetation cover is more or less continuous over the reef islands of Nui Atoll, being composed principally of scrub or woodland of Pisonia or coconuts. There are no extensive areas bare of vegetation as on drier atolls, such as in Kiribati to the north. The sparse scrub communities occur largely on unfavourable substrates; the Scaevola scrub is sparse on the rubble ridges of north west Meang, and Pemphis scrub is sparse in low lying areas central to several reef islands which seem to represent old inter-island channels and which are probably liable to infrequent inundation. Suriana does not occur as a distinct scrub unit, as in the Cook Islands, but as isolated shrubs.

The vegetation has been modified by human disturbance. Clearing of scrub from beneath coconut woodland is common practise around the village and was observed to have occurred on many other plots. Collection of domestically important plants almost certainly accounts for the present distribution of these plants; for instance the edible fern Asplenium is rare close to the settlement on Fenua Tapu, even in Pisonia woodland where it might be expected, and where it does occur is more commonly epiphytic than growing on the ground. It is much more common on islands further from the main village where it grows both epiphytically and on the ground. Pandanus leaves are also likely to have been collected intensively close to the settlements, and Pandanus is a much less obvious component of scrubland on Fenua Tapu than elsewhere. The main area for collection of Pandanus leaves was on Meang in 1982.

The flora is composed of plants that have a widespread distribution throughout the Pacific and is similar to that recorded in Kiribati, the Tokelau Islands or on other islands in Tuvalu. Neither Thespesia populnea nor Hibiscus tiliaceus were recorded on Nui, though both occur on neighbouring Vaitupu and were collected on Nanumea to the north. Ximenia americana appears to be found only on the northern islands of Tuvalu, and has not been observed on the southern atolls.

It is interesting that Acalypha amentacea var. is such a prominent element of the flora of the scrublands, growing with Scaevola. Acalypha is not recorded as such a common element of scrublands outside Tuvalu; it is frequent on Vaitupu, but is restricted to one occurrence on Nukulaelae where it was introduced for compost for the pulaka pits.

There are a lot of introduced plants on Fenua Tapu, where garden crops, ornamentals and weeds have been introduced, but there are many less exotics than on Vaitupu or Funafuti.

References

- Chambers, A. 1975 Nanumea Report. A socio-economic study of Nanumea Atoll, Tuvalu. Victoria University of Wellington.
- David, Mrs Edgeworth 1899 Funafuti or three months on a coral atoll: an unscientific account of a scientific expedition. London. John Murray.
- Fosberg, F.R. 1953 Vegetation of Central Pacific Atolls, a brief summary. Atoll Res. Bull. 23, 1-26.

- Fosberg, F.R. 1960 The vegetation of Micronesia. 1. General descriptions, the vegetation of the Marianas Islands, and a detailed consideration of the vegetation of Guam. Bull. Am. Mus. Nat. Hist. 119, 1-76..
- Gressitt, J.L. 1952 Description of Kayangel Atoll, Palau Islands. Atoll Res. Bull. 14, 1-5.
- Hedley, C. 1896 General account of the atoll of Funafuti. Mem. Aust. Mus. 3, 1-71.
- Koch, G. 1961 Die materielle Kultur der Ellice-Inseln. Veröff. Museums für des Völkerkunde, Berlin. N.F.3, 199pp.
- Linton, A.M. 1933 Notes on the vegetation of Penrhyn and Manihiki Islands. J. Polynes. Soc. 42, 300-307.
- Luomala, K. 1953 Ethnobotany of the Gilbert Islands. Bishop Mus. Bull. 213, 129pp.
- Maiden, J.H. 1904 The botany of Funafuti, Ellice Group. Proc. Linn. Soc. N.S.W. 29, 539-556.
- Marshall, M. 1975 The natural history of Namoluk Atoll, Eastern Caroline Islands. Atoll Res. Bull. 189, 1-53.
- Moul, E.T. 1957 Preliminary report on the flora of Onotoa Atoll, Gilbert Islands. Atoll Res. Bull. 57, 1-48.
- Niering, W.A. 1961 Observations on Puluwat and Gaferut, Caroline Islands. Atoll Res. Bull. 76, 1-10.
- Parham, B.E.V. 1971 The vegetation of the Tokelau Islands with special reference to the plants of Nukunono Atoll. N.Z. Jl. Bot. 9, 576-609.
- Small, C.A. 1972 Atoll agriculture in the Gilbert and Ellice Islands. Department of Agriculture, Tarawa, 154pp.
- Stoddart, D.R. 1975 Vegetation and floristics of the Aitutaki motus. Atoll Res. Bull. 190, 87-116.
- Sykes, W.R. 1976 Vegetation of Palmerston Atoll. Unpubl. Report Botany Division, DSIR, Christchurch.
- Whistler, W.A. 1983 The flora and vegetation of Swains Island. Atoll Res. Bull. 262, 1-25.
- Woodroffe, C.D. and Moss T.J. 1984 Litter fall beneath Rhizophora stylosa Griff., Vaitupu, Tuvalu, South Pacific. Aquatic Botany, 18, 249-255.

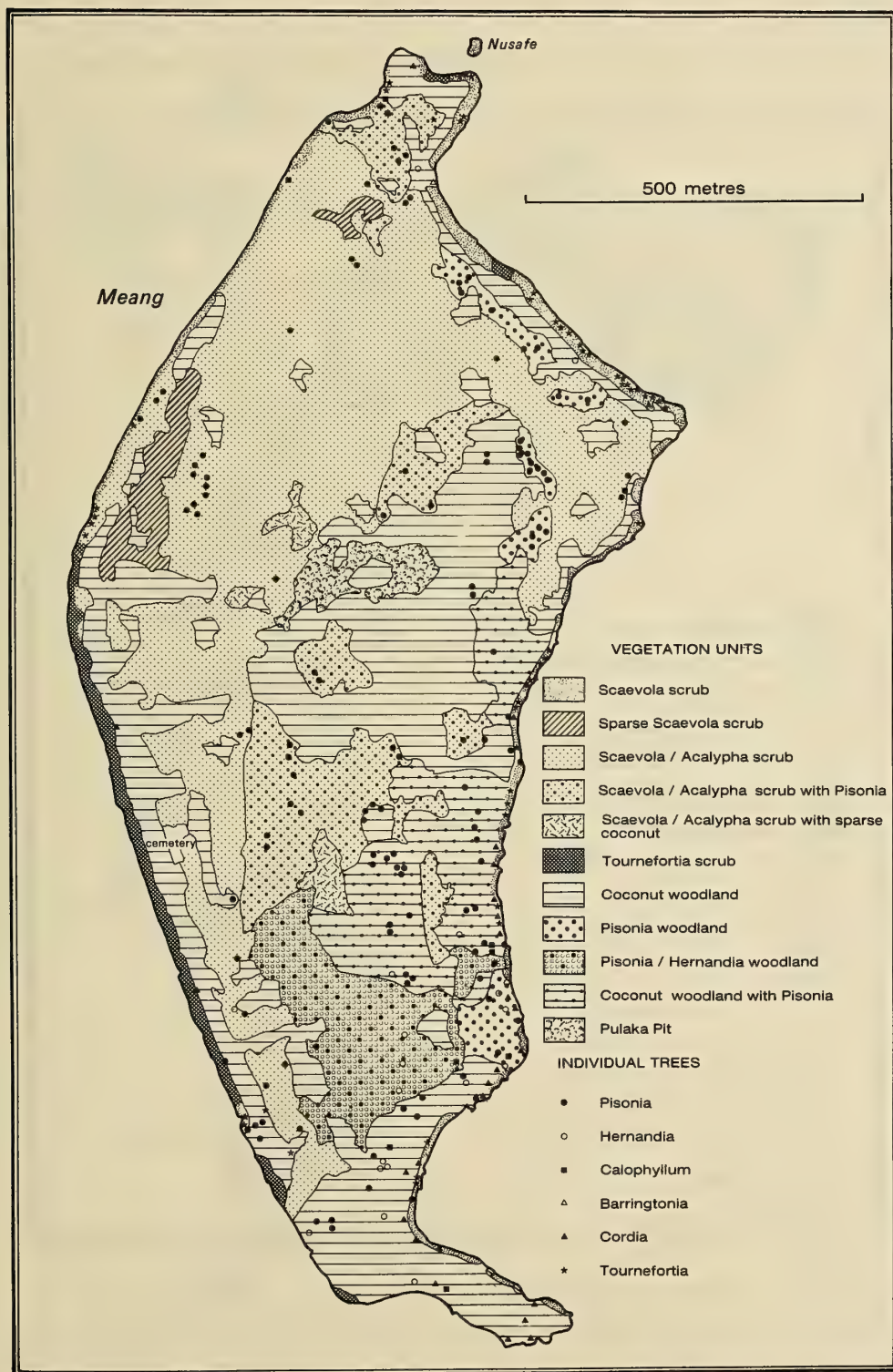


Fig. 2. Vegetation of Meang and Nusafe



Fig. 3. Vegetation of Tokinivae, Tokinivae 2 and Tokinivae 3

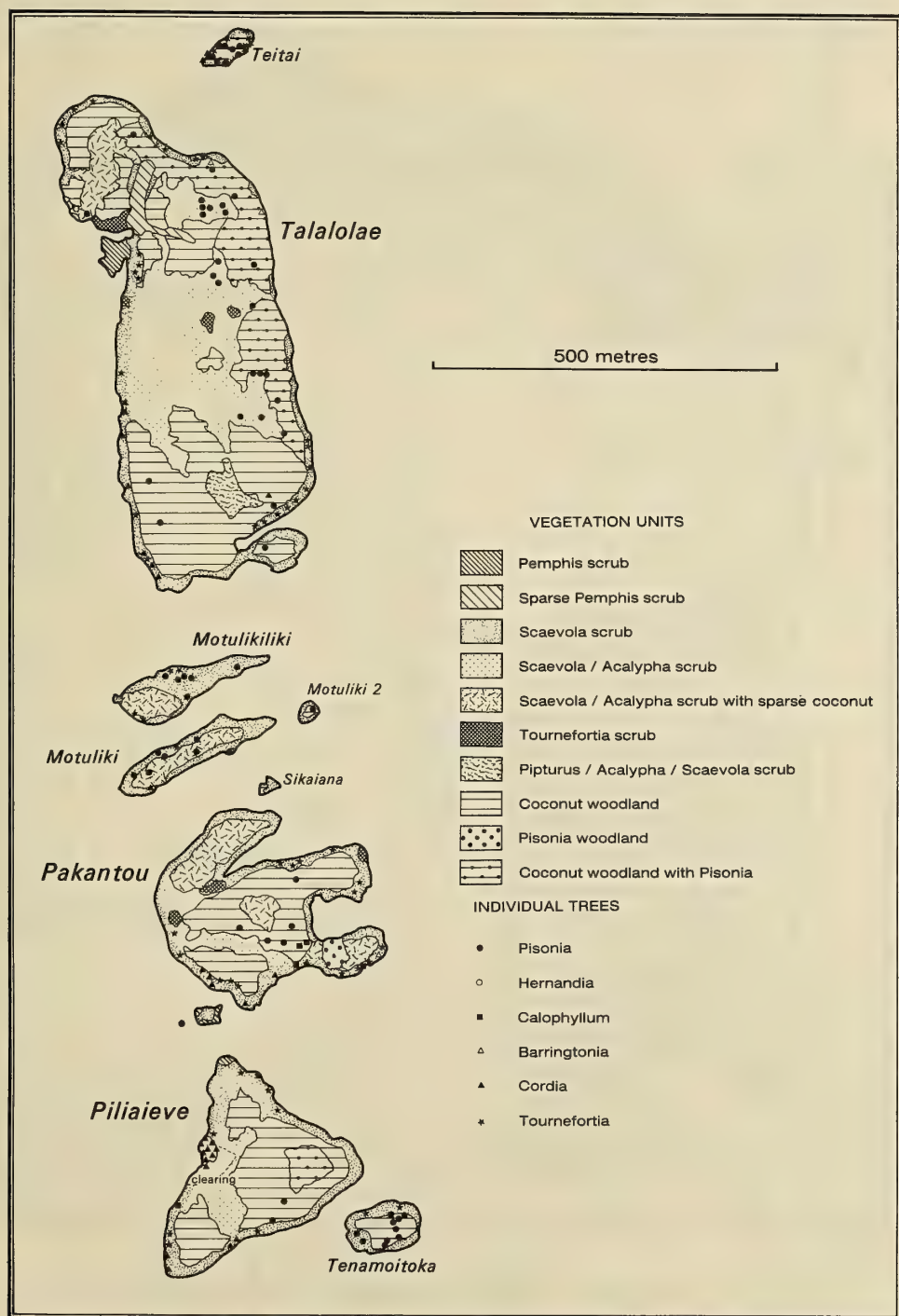


Fig. 4. Vegetation of Teitai, Talalolae, Motulikiliki, Motuliki, Motuliki 2, Sikaiana, Pakantou, Piliaieue and Tenamoitoka



Fig. 5. Vegetation of Unimai, Unimai 2, Kokole, Pongalei and Motupuakaka

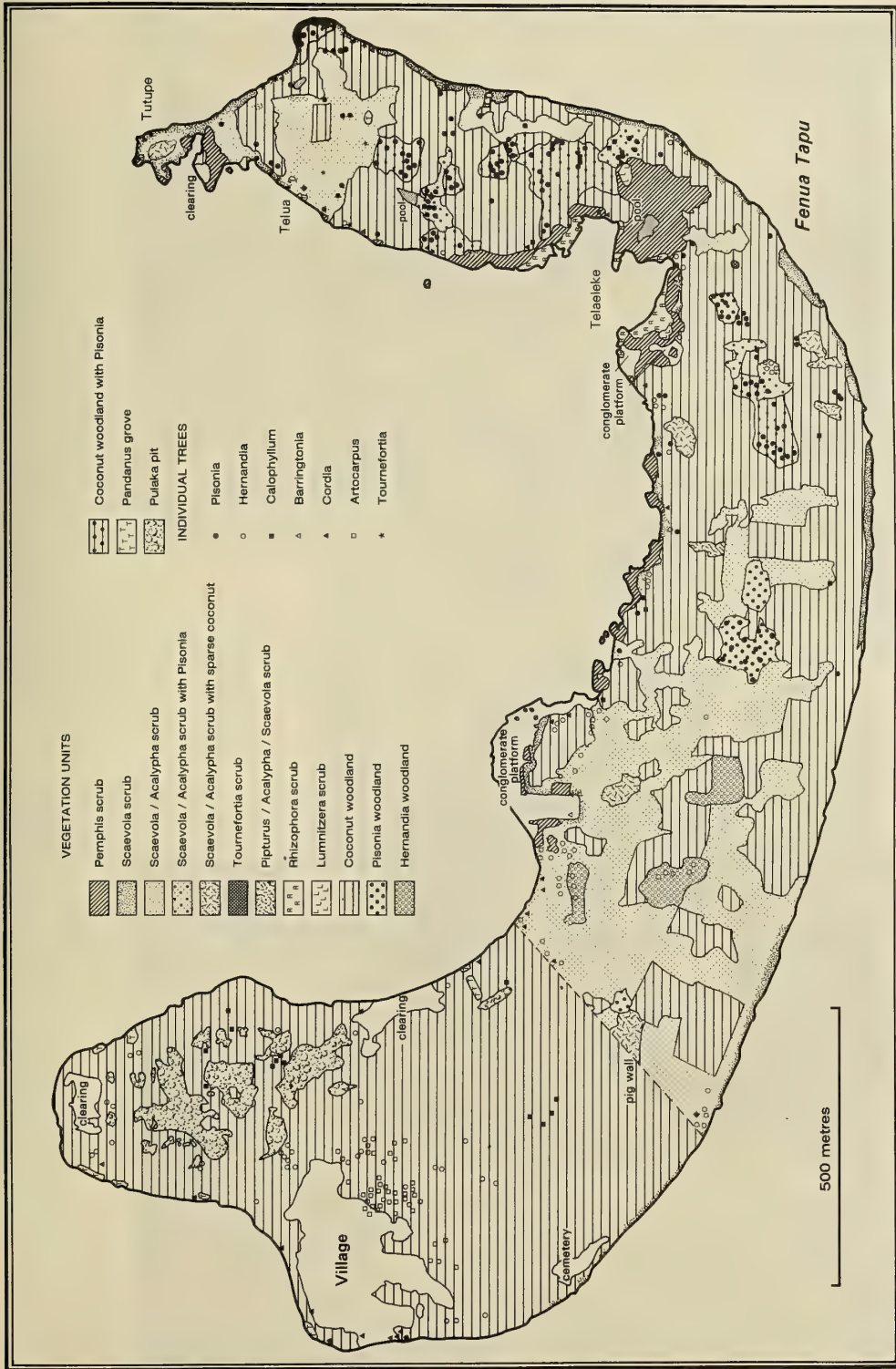


Fig. 6. Vegetation of Fenua Tapu



Plate 1. Pemphis scrub, western Tokinivae



Plate 2. Scaevola scrub on recently formed beach ridge, northeastern Fenua Tapu

Plate 3. Sparse Scaevola scrub, on fine rubble substrate, western Meang





Plate 4. Coastal Tournefortia scrub, western shore of Meang



Plate 5. Pipturus/Acalypha/Scaevola scrub, with young Guettarda in foreground, eastern Fenua Tapu



Plate 6. Coconut woodland with Asplenium,
western Tokinivae



Plate 7. Pisonia woodland, Unimai



Plate 8. Scaevola/Acalypha scrub with coconuts, Unimai

ATOLL RESEARCH BULLETIN

No. 284

INITIAL RECOLONIZATION OF FUNAFUTI
ATOLL CORAL REEFS DEVASTATED BY
HURRICANE "BEBE"

By

HANS MERGNER

ISSUED BY

THE SMITHSONIAN INSTITUTION

WASHINGTON, D. C., U.S.A.

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INITIAL RECOLONIZATION OF FUNAFUTI
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Abstract

On the 21st of October, 1972, hurricane "Bebe" devastated a large part of Funafuti atoll in the Ellice Islands. Among the most spectacular geomorphological alterations caused by the hurricane was a storm beach 19 km long, 4 m high and 37 m wide. The amount of coral debris washed up from the offshore coral reefs onto the reef flat was estimated at 2.8×10^6 tons of material (Baines, Beveridge and Maragos, 1974). The oceanside reef communities of the SE and E rim of the atoll had been totally destroyed, and those of the inner reefs of the lagoon side had been heavily damaged. Eight months after the storm a quantitative analysis of the resettlement and recruitment of coral species on 7 reef sections was carried out: the destruction of the biophysiographic zones could be described as increasing from the northern border and also to the W rim of the atoll. Near the centre at Fongafale the lagoon reef flat was covered by thick carpets of the brown alga Dictyota bartaysii, possibly brought about by eutrophication effects. The resettlement of the reef flat by corals began with the recolonization of branching corals as well as regeneration of the very few surviving massive corals: about 80% of the number of new colonies belong to Acropora (mainly A. humilis and A. hyacinthus), and about 20% to Pocillopora eydouxi, Porites lutea (?) and some Faviidae. The percentage of the area settled by the massive coral species is, however, greater than that settled by the branching species. Nevertheless, in the long-term, branching corals are expected to have a decisive influence on the future structural and biophysiographic zonation of the reef edge and reef flat, due to their more numerous young colonies, which are evenly scattered over the reef area, and due to their rapid growth rate. Consequently, an Acropora humilis - hyacinthus-community or an Acropora - Pocillopora eydouxi-assemblage can be predicted as the future biophysiographic zone.

Introduction

On the 21st of October, 1972, hurricane "Bebe" devastated a large part of Funafuti atoll, Ellice Islands (now Tuvalu) in the Southwestern Pacific. Six weeks later, December 10-24, 1972, Maragos, Baines and Beveridge (1973) investigated the geomorphological alterations caused by the cyclone especially on the SE side of the Atoll. A storm beach 19 km long, nearly 4 m high and 37 m wide was the most conspicuous geomorphological change. The amount of coral debris washed up from depths down to 20 m and onto the reef flat was estimated at 2.8×10^6 tons of material and was derived from the outer reefs of this side which had been totally destroyed. In addition, the inner reefs of the lagoon side had also been heavily damaged. The authors gave a detailed report and some personal comments on the alterations which they found and the condition of the reefs at the Second International Coral Reef Symposium in Brisbane, 1973 (Baines, Beveridge and Maragos, 1974). These were used as a basis for the planned investigation on the recolonization of the destroyed reefs.

Observations on the effects of tropical cyclones have been published by Blumenstock (1958, 1961) and Blumenstock et al. (1961), McKee (1959), Stoddart (1963, 1965, 1974), Tunnicliffe (1981), Woodley et al. (1981) and others. New growth and recolonization of corals have been described among others by Fishelson (1973), Loya (1976a, 1976b), Mergner (1979, 1981), Pearson (1981) and Schumacher (1977). Scientific descriptions of Funafuti atoll and its geology have been given by David and Sweet (1904), and as to the biology of the reef-forming organisms by Finckh (1904).

In July (6-11), 1973, 8 1/2 months after the hurricane, and just after the Symposium, I carried out the first quantitative analysis of the recolonization of some reef sections of the atoll. For the purposes of comparison, several regions of the reef both flourishing and partly damaged, were investigated. The following is a report of these investigations.

Seven sections examined on Funafuti reefs

Funafuti atoll (Fig. 1) is located on the undersea ridge of the Ellice Islands about 1000 km north of the Fiji-Archipelago arising from a depth of more than 4000 m. It consists of 29 coral islands differing greatly in size, sometimes oblong in shape, sometimes round and very small, and covered with forest (Cocos nucifera, Pandanus tectorius, Pisonia grandis and others). The islands are connected by reef barriers and form a rectangle with one elongated corner (Fig. 2). Aside from numerous shoals, nine outlets (locally called "Te Ava") connect the open sea with the lagoon, which reaches a depth of 54 m at two positions and flattens to a few meters especially in the south. Some of the passages are navigable: in 1899 Agassiz (1903) had entered two of them on board the research vessel "Albatross".

The Centre of hurricane "Bebe" struck the SE side of the atoll in October, 1972, and thus caused the greatest damage to the reefs located there (see Baines, Beveridge and Maragos, 1974). But the reefs of the NE side and of the S tip also suffered conspicuous damage in contrast to those of the SW and NW sides, which showed only few or nearly no effects of the storm because they had been better protected by the sheltering eastern reefs and the atoll lagoon. According to these criteria, the test areas and the reefs for comparison purposes had to be selected (Figs. 1, 12).

Two sections were selected for the N rim of the destruction zone close to the N end of the isle of Tengako (sections 1 and 2), two for the S rim of this zone near the isle of Tutanga at the S end of the atoll (sections 6 and 7), two for the W side of the atoll lagoon near the isle of Faufatu at the W end of the atoll (sections 4 and 5) and one for the centre of the destruction zone near the E end of the main island Funafuti (section 3). Because of the high swell from the east and correspondingly high breakers, the exposed outer reef section could not be investigated.

In all sections, the biophysiographic zonation was studied in a strip 20 to 100 m wide from the sea-shore across the reef flat to the fore reef or the lagoon floor. The distances from the mean water level to the reef edge were between 120 and 250m; greater distances could not be reached by snorkeling.

In contrast to reef sections 4-7, which showed no or only little damage, nearly the whole reef flat of sections 1-3 had been destroyed. Here, in each case, a test area of 20 x 20 m or 20 x 10 m was marked with plastic lines extending from the lagoon floor or reef slope over the reef edge onto the outer reef flat. Within the borders of each area all living remains of former coral colonies (without exception, e.g. massive or crustose species) and newly settled colonies were marked on a map and their sizes were calculated by taking the average between the longest and shortest diameters. All drawings, measurements and underwater photographs were made by snorkeling down to a depth of 5 m.

Results of zonation studies of reef sections 1-7

First, the structure, the flora and fauna and the biophysiographic zonation of all reef sections investigated will be briefly characterized. Then, the recolonization of the reef platforms will be analyzed using reef sections 2 and 3 as examples.

Reef section 1

Reef section 1 is situated at the N rim of the central destruction zone of hurricane "Bebe", and 300 m south of the N end of the isle of Tengako. It extends SW from the shore of the lagoon for 160-180 m with a minimum breadth of 20 m, and its zonation is shown in Table 1, Fig. 12.

Reef section 1 shows serious damage to the reef platform and reef edge. Its biophysiographic zonation is characterized by sparse growth of different algae species on the abraded reef flat. Within more than 500 m² of the reef front, only 17 massive faviid colonies had survived, but no scleractinian colony had resettled. Aside from a few Pagurids and fishes no mobile fauna is visible.

Reef section 2

Section 2 (Fig. 3) runs parallel to and about 1200 m from section 1 and is located nearer the centre of the hurricane "Bebe" zone. It runs in a SW direction, is 140 m long and has a minimum

breadth of 20 m. In many respects, its structure, settlement and zonation are similar to those of section 1. It does, however, differ from section 1 in that there is--aside from some remainders of dead coral colonies--a total lack of surviving living colonies. There are many species of fish in this area and, above all, there is a recolonization of numerous young scleractinian colonies (Table 2, Fig. 12).

Reef section 2 had been damaged to a greater extent by the hurricane than section 1: the old reef flat was largely eroded, the reef edge destroyed and its *Acropora*-zone totally demolished. No coral colony survived, but within 136 m² of the reef front 84 young coral colonies had resettled. The fish fauna is much more plentiful than in section 1, both in numbers and in species.

Reef section 3

Reef section 3 is situated in the middle of the central destruction zone of hurricane "Bebe", 120 m SW of the small jetty of Fongafale on Funafuti Island. It covers the inner reef of the lagoon side with a length of 120 m and a breadth of 20 m westward. Possibly due to the eutrophication by sewage of the surface water, which is only slightly agitated, a thick layer of the brown alga *Dictyota bartaysii* (Fig. 4) loosely covering the reef flat has developed. It largely conceals the serious damage due to the storm and allows only fragmentary insights into the settlement structures of this section. However, on alga-free coral rock areas along the reef edge large numbers of young stony coral colonies have resettled (Table 3, Fig. 12).

Of all the reef sections investigated, section 3 was hit the hardest by the hurricane. Aside from damage caused by hurricane "Bebe", much of this area has been changed during World War II. In addition, large areas of the reef edge and the reef slope are covered with dense algal carpets that have probably resulted from eutrophication effects of sewage. Nowhere can uninjured surviving stony corals be found; living faviid colonies can only be found in limited areas. However, 67 coral colonies, mostly species of *Acropora*, have resettled on the alga-free areas along the reef edge, covering an area of nearly 50 m². The occurrence of numerous herbivorous and detritophagous fish species like Acanthuridae, Chaetodontidae, Mullidae and Pomacentridae probably should be attributed to the mass population explosion of the algal stocks.

Reef section 4

Reef section 4 (Figs. 5-7) extends eastward from the NE end of the horseshoe-like island of Faufatu in the middle of the W side of the atoll. It runs for a length of 120 m and a maximum breadth of 100 m through the inner reef but does not reach the reef edge. In

spite of its location facing the path of hurricane "Bebe", the storm damage--apart from some overthrown colonies of Acropora hyacinthus--is minimal, because the section is protected by an extensive reef platform located on its E side. This section is therefore suitable for comparison with the greatly damaged reef sections 1-3. Quantitative investigations of surviving and resettled young coral colonies were not necessary. Because of the breadth of section 4, it is differentiated into a northern (N), a middle (M), and a southern (S) strip in Table 4 when necessary (Table 4, Fig. 12).

Generally speaking, reef section 4 is a suitable example of an undamaged inner reef with characteristic coral assemblages and biophysiographic zones. The reef edge with its coral communities at a distance of more than 800 m could not be reached by swimming because of the strong currents. However, a strong current of 25 cm/s also occurred within the shore channel, and here similar assemblages, among others a well-developed Acropora hyacinthus (Pocillopora eydouxi)-zone, have settled. Their species composition should be comparable with those of the former zones of reef sections 2 and 3 before their destruction by the hurricane. Fishelson (1973), Loya (1976a) and Mergner (1981) have shown that damage caused by man-made perturbations and natural catastrophes will be gradually erased by regeneration and recolonization of the coral colonies if no further perturbation is added. Therefore, the expectation that the destroyed zones will gradually regain their former structure and species composition is also justified in this case.

Reef section 5

Reef section 5 begins at the curved south side of the isle of Faufatu, 250 m south of reef section 4. It covers the outer reef with a length of 120-180 m and a maximum breadth of 80 m to the SSW up to the surf zone (Table 5; Figs. 7, 12).

This reef section shows the typical zonation of the southwest Pacific outer reef. Because of the strong surf, reef slope and fore-reef could not be inspected. The storm damage seems to be relatively small. Thus, reef section 5 is a good comparison for the destroyed outer reefs of the E side of the atoll.

Reef section 6

Reef section 6 (Fig. 9) also belongs to the outer reefs of the W side of the atoll. It begins near its southern end on the SW edge of the isle of Tutanga and runs westwards for 150 m with a breadth of 50 m to the upper reef slope. Because of its location on the lee-side of the path of hurricane "Bebe" and at the most extreme S edge of its destruction zone, the damage is minimal. The surface current was very rapid (40 cm/s), but the surf of this reef

site was weak during the investigation period. Therefore, a short study of the coral assemblages in the region between reef edge and fore reef was possible (Table 6, Fig. 12).

Reef section 6 shows a characteristic boulder zone: the large coral blocks were apparently thrown up by storm waves of former cyclones coming from westerly directions. They are even cited in David and Sweet (1904). The coral assemblages of the greatly cleft reef edge and the steep reef slope with its deep spurs and grooves are very diversified. Both zones characterize this reef section, which combined with the zonation of the reef flat in section 5, gives an approximate impression of the original appearance of the outer reefs destroyed on the eastern atoll side.

Reef section 7

Reef section 7 (Figs. 9, 11) covers 160-200 m of the inner reef, is 50-70 m wide and runs from the SE corner of the isle of Tutanga towards the SE. Just as outer reef section 6, section 7 is influenced by a strong surface current of at least 25 cm/s flowing from the lagoon outwards to the open sea. In spite of its location at the S edge of the destruction zone of hurricane "Bebe", no serious storm damage can be observed along this section. Possibly, the narrow south tip of the atoll lagoon did not provide a long enough fetch (only 1.5 km) with enough water (it is very shallow here) for the hurricane to build up large enough waves to cause extensive damage. Section 7 thus gives the impression, just as section 4, that it is an intact inner reef. Its biophysiographic zonation, however, differs in many respects from that of section 4 and all other inner reef sections by the prevalence of microatolls, especially of *Porites lutea*, and by the lack of a characteristic reef slope (Table 7, Fig. 12).

Seen as a whole, section 7 is of less interest for a comparison between undestroyed and destroyed inner reefs.

Results of the quantitative analysis of reef sections 2 and 3

All the inner and outer reef sections investigated on the W and SW side of Funafuti atoll (4-7) proved to be relatively undamaged and generally suitable models for comparison with the seriously damaged reefs of the E side. This is especially true for section 4 as an inner reef and a combination of sections 5 and 6 as model of an outer reef (Fig. 12).

Thus, the reef flat of outer reef section 5, within the area of the abrasion zone, the shingle zone and the algal ridge, shows typical features of the zonation of SW Pacific atolls. In addition, its remaining coral zone in the region bordering on the algal ridge indicates the former existence of large stocks of the *Halimeda-Montipora foliosa*-community. However, the boulder zone on the reef flat, which is almost always present, is lacking in

section 5, but well developed in outer reef section 6. The reef edge and upper reef slope of this section show the characteristic species composition of their coral assemblages. Therefore, a combination of the zonation of both sections probably offers a true representation of the sequence of zones on a W outer reef on Funafuti atoll. Unfortunately, this view could not be compared with the present aspect of the destroyed outer reefs on the E side. For details of their former aspect see the contributions of "The Atoll of Funafuti" (1904) and for the situation immediately after the hurricane see Baines, Beveridge and Maragos (1974).

An impression of the later result of the recolonization of the eastern inner reefs can be formed much more easily by examining the coral zones of western inner reef section 4: these zones are characterized by Acropora humilis-hyacinthus and Pocillopora eydouxi-communities, but not by massively growing faviids and poritids, which, in spite of early regeneration of the surviving colonies, are less important as predominant species compared with Acropora and Pocillopora. In contrast to that of section 4, the zoning of section 7 is less helpful for comparison with damaged inner reef sections 2 and 3, because it is characterized by microatoll formations especially of Porites lutea. Only isolated areas of the immediate reef edge are settled by typical Acropora-Pocillopora-communities. Conspicuous in both inner reef sections of the western side (4 and 7) is the almost complete lack of macroalgae on the reef flat, whereas on the inner reefs of the eastern side luxuriant algal stocks have developed.

All three reef sections investigated on the E side of Funafuti atoll must be considered as largely damaged by storm, with the extent of damage increasing from the northern border (reef sections 1 and 2) to the central destruction zone (section 3). An initial comparison of the three sections shows that, in the northernmost section a number of massively growing Plesiastrea colonies had indeed survived, but no new colonization was observed. On the other hand, in the more southerly sections 2 and 3, no colonies survived without damage and only smaller regenerating areas have arisen, but, at the same time, numerous young colonies of different size have initiated the first phase of recolonization (Figs. 13, 14). Almost all of these pioneer species belong to Acropora, a few to Pocillopora and Porites, and some to the faviids.

In order to verify results on species composition, species diversity, and settling density during the first phase of the recolonization, a careful quantitative analysis within the area of the reef edge and the close reef flat of both sections is necessary.

Reef section 2

Quantitative study of recolonization in reef section 2 (Fig. 13) consisted solely of enumerations and measurements of the

resettled and regenerated areas of the scleractinians within a strip, 8 to 15 m wide behind the reef edge. In this area of about 136 m², for reasons of simplification, all holes and channels with sandy bottom or debris were included, although these are usually not colonized. Thus, the area actually colonized should be reduced by about 25%.

Within the area studied, 84 stony coral colonies were counted belonging to the following genera and species:

<u>Acropora</u> (<u>corymbosa</u> , <u>humilis</u> , <u>hyacinthus</u>)	67 colonies = 79.7%
<u>Goniastrea</u> (<u>retiformis</u>)	12 colonies = 14.3%
<u>Platygyra</u> (<u>lamellina</u>)	1 colony = 1.2%
<u>Pocillopora</u> (<u>damicornis</u> , <u>eydouxii</u>)	2 colonies = 2.4%
<u>Porites</u> (<u>lutea</u>)	2 colonies = 2.4%
<u>Scleractinia</u>	84 colonies = 100.0%

It is possible that some growth areas of Goniastrea originate from several regenerating segments of a formerly uniform larger colony, but this is not likely in the case of an Acropora humilis colony 30 cm in diameter. All remaining coral heads with smaller diameters may be considered as young colonies that settled during the 8 1/2 months after the passage of hurricane "Bebe" and since then have continued to develop, to reach varying and often considerable sizes. According to the time of settling the following diameters (\emptyset) and base areas of Acropora were determined:

6 colonies with up to 2 cm \emptyset and 3.1 cm ² ,	altogether 18.6 cm ²
14 colonies with 2.5- 3 cm \emptyset and 7.1 cm ² ,	altogether 99.4 cm ²
27 colonies with 3.5- 5 cm \emptyset and 19.6 cm ² ,	altogether 529.2 cm ²
10 colonies with 5.5- 8 cm \emptyset and 50.2 cm ² ,	altogether 502.0 cm ²
8 colonies with 8.5-10 cm \emptyset and 78.5 cm ² ,	altogether 628.0 cm ²
1 colony with 10.5-15 cm \emptyset and 176.6 cm ² ,	altogether 176.6 cm ²
1 colony with 15.5-30 cm \emptyset and 706.5 cm ² ,	altogether 705.5 cm ²
67 colonies with a settling area of altogether	2660.3 cm ²

By contrast, only 12 young colonies or regenerating segments of the massively growing Goniastrea inhabit 4979 cm², an area twice as large as that occupied by Acropora. The other 5 newly settled colonies, covering 528 cm² (Platygyra with 314 cm², Pocillopora with 157 cm² and Porites with 57 cm²) are less significant for the recolonization of the reef area analyzed, which totals ca. 8168 cm². Of 136 m² of the area concerned, the 84 young colonies occupy only about 0.6%, which can be divided up as follows:

<u>Acropora</u>	with 67 colonies and 2660 cm ²	area amounts to 0.20 %
<u>Goniastrea</u>	with 12 colonies and 4979 cm ²	area amounts to 0.37 %
<u>Platygyra</u>	with 1 colony and 314 cm ²	area amounts to 0.02 %
<u>Pocillopora</u>	with 2 colonies and 157 cm ²	area amounts to 0.01 %
<u>Porites</u>	with 2 colonies and 57 cm ²	area amounts to 0.004%

Scleractinia with 84 colonies and 8168 cm² area amount to 0.60 %

Goniastrea retiformis dominates all other coral species regarding its share of the settling area, but is not dominant in its significance for the future structural and biophysiological zonation. The Acropora species, with their 67 young colonies equally distributed over this reef segment, are much more important and will influence the later appearance of the reef edge and the neighboring reef platform. There are two reasons for this: first, Acropora species grow much more rapidly than the massive colonies of Goniastrea, and are also able, because of their favorable distribution, to roof over the area of settlement within a relatively short period. Therefore, they are at an advantage over all the others in the competition for space and light. Second, they form a varied landscape with their diversified structures providing numerous hiding places and a good food source as the biocenosis for many different species of reef fauna.

It can be assumed, and comparable observations from Red Sea coral reefs (Fishelson 1973, Loya 1976a, Mergner 1981) substantiate this assumption, that further undisturbed development will result in the establishment of an Acropora humilis-hyacinthus-zone as the biophysiological zone of the reef edge and neighboring reef flat, such as found in other reef regions of Funafuti atoll, as in reef section 4 for example (Fig. 7).

Reef section 3

In reef section 3 (Fig. 14), all newly-settled and regenerating stony corals were also enumerated, measured and exactly marked on underwater maps. However, here only a narrow strip, 2.5 m wide on the average along the reef edge, could be mapped, because large reef areas were covered by carpets of the brown alga Dictyota bartaysii (Fig. 4), and all new-settled stony coral colonies were found only on algal-free coral rock. In the test area of about 50 m², 67 young colonies were found belonging to the following genera (with species names):

<u>Acropora</u> (<u>humilis</u> , <u>hyacinthus</u> , <u>pulchra</u> etc.)	50 colonies = 74.6%
<u>Faviidae</u> (<u>Favia</u> , <u>Goniastrea</u> etc.)	7 colonies = 10.5%
<u>Pocillopora</u> (<u>damicornis</u> , <u>eydouxii</u>)	7 colonies = 10.5%
<u>Porites</u> (<u>lutea</u>)	3 colonies = 4.4%
<u>Scleractinia</u>	67 colonies = 100.0%

Only one faviid colony can be assumed to be newly settled, the other 6 are regenerating parts of a former larger colony. Such an origin can also be assumed for one Porites lutea colony and possibly one for Acropora colony with a diameter of 20 cm. All the other coral heads are young colonies that have settled since the passing of hurricane "Bebe". The following diameters (\emptyset) and base areas corresponding to the time of settling have been ascertained for Acropora:

3 colonies with up to 1 cm \emptyset and	0.8 cm ² ,	altogether	2.4 cm ²
9 colonies with 1.5- 2 cm \emptyset and	3.1 cm ² ,	altogether	27.9 cm ²
16 colonies with 2.5- 3 cm \emptyset and	7.1 cm ² ,	altogether	113.6 cm ²
14 colonies with 3.5- 5 cm \emptyset and	19.6 cm ² ,	altogether	274.4 cm ²
2 colonies with 5.5- 8 cm \emptyset and	50.2 cm ² ,	altogether	100.4 cm ²
4 colonies with 8.5- 10 cm \emptyset and	78.5 cm ² ,	altogether	314.0 cm ²
1 colony with 10.5- 15 cm \emptyset and	176.6 cm ² ,	altogether	176.6 cm ²
1 colony with 15.5- 20 cm \emptyset and	314.0 cm ² ,	altogether	314.0 cm ²
<hr/> 50 colonies with a settling area of altogether			1323.2 cm ²

By contrast, only 6 regenerating and one young faviid colony cover an area of 7870 cm², which is nearly 6 times more than Acropora; Porites, which also grows massively, with only one regenerating and 2 young colonies, covers 648 cm², which is half that occupied by Acropora. The branched coral Pocillopora claims 563 cm² for 7 young colonies. Thus, the total area recolonized by corals amounts to 10403 cm². Based on 50 m² of the reef area analyzed along the reef edge, the recolonization involves about 2%, which can be divided up as follows:

<u>Acropora</u>	with 50 colonies and 1323 cm ²	area amounts to 0.26%
<u>Faviidae</u>	with 8 colonies and 7870 cm ²	area amounts to 1.57%
<u>Pocillopora</u>	with 7 colonies and 563 cm ²	area amounts to 0.11%
<u>Porites</u>	with 3 colonies and 648 cm ²	area amounts to 0.13%

In reef section 3 it is much more evident than in reef section 2 that the area covered by the massive stony corals (Favia, Goniastrea, Porites) is much larger than that covered by the branched corals (Acropora, Pocillopora). But regardless of this fact, the latter corals will definitely influence the future structural and biophysiological zonation of the reef edge. The rapidly growing Acropora species will soon predominate in this reef area both numerically and physiologically and together with Pocillopora will build up a varied biocenosis for a reef fauna rich in species and numbers. A condition favoring this is the high initial settling density along the reef edge in section 3: on each square meter of free coral rock 1.14 young colonies of branched

corals settle, compared to only 0.5 colonies in reef section 2. It cannot be proved that this is due to the reduced amount of free settling area resulting from the unusual proliferation of algae. With further undisturbed development, an Acropora humilis-hyacinthus-zone or a mixed Acropora-Pocillopora-zone, will also develop in section 3 as the biophysiographic zone of the reef edge and neighboring reef platform. Estimates differ as to the time required for this development. However, further damage caused by new storms and/or by man's influence may change or delay or even prevent this evolution.

Conclusions

1. The geomorphological alterations of large parts of Funafuti atoll caused by hurricane "Bebe" have been described by Baines, Beveridge & Maragos (1974). Here some reef sections destroyed on the E side are compared with undestroyed sections on the W and SW side, and the first phase of the recolonization of two reef areas by stony corals is analyzed.
2. The extent of the damage to the reef sections studied can be ascertained by the alterations of their structure and biophysiographic zonation: it increases from the northern border zone of the cyclone (reef sections 1 and 2) to the central destruction zone where section 3, close to Fongafale, had been most intensively struck. Wide areas of its devastated reef flat are covered by thick carpets of the brown alga Dictyota bartaysii possibly because of eutrophication.
3. Quantitative analyses in destroyed reef regions 2 and 3, show that recolonization by scleractinians is a result of regenerating segments of the few surviving massive coral colonies and of newly settling branched corals. Among them Acropora humilis and A. hyacinthus (and with reservations also A. corymbosa, formosa and pulchra) and Pocillopora eydouxi are especially prominent: Acropora comprises 79.7% (sect. 2) to 74.6% (sect. 3) of the number of all young colonies, Pocillopora 2.4% (sect. 2) to 10.5% (sect. 3). However, the massive growth species outweigh the branched corals with respect to percentage of area settled; the massive growth species occupy 0.4% to 1.7% of the entire area, while the branched corals occupy only 0.2% to 0.4%.
4. In spite of this, the branched corals will have a decisive influence on the future structural and biophysiographic zonation of the reef edge and the neighboring reef flat. This is indicated by the fact that their young colonies are much more numerous and evenly distributed over the area to be settled and by their large initial settling density (0.5 to 1.14 young colonies for each square meter of free coral rock area). This initial advantage and their more rapid growth rate causes them to form a varied coral landscape within a relatively short period of time with diversified

hiding places and food sources providing niches for a reef biocenosis rich in species and numbers.

Thus, it is predicted (as in comparable structures in Red Sea coral reefs) by the indicator species present, that with further undisturbed development, an Acropora humilis-hyacinthus-assemblage or an Acropora-Pocillopora eydouxi-community will develop into the future biophysiographic zone of the reef edge and the neighboring reef flat.

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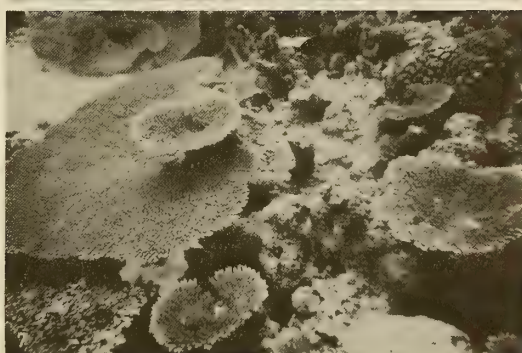
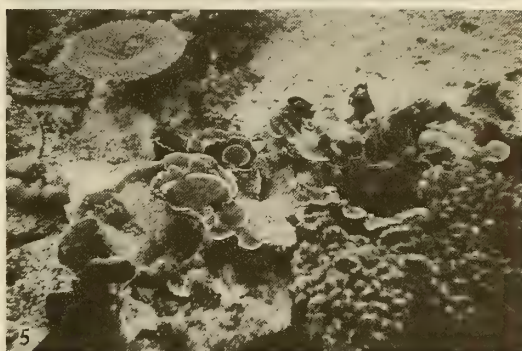
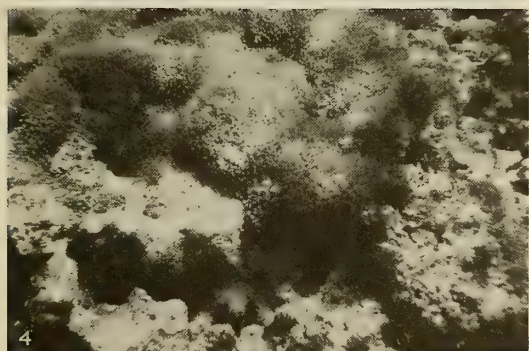
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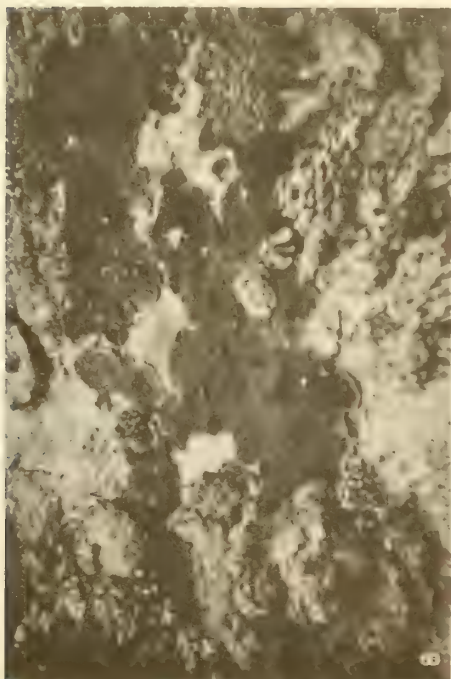
References

- Aerial Photos of Ellice Islands. Film I, 11th of July, 1971, No. 73/74 (18,000 ft.): 137/206, 159/160, 178/179, 188/189 (all: 5,000 ft., scale 1:10,000). Directorate of Overseas Surveys, Surrey, Great Britain.
- Agassiz, A. (1903): The coral reefs of the tropical Pacific. Memoirs Mus. Comp. Zool. at Harvard College, 28: Cambridge, U.S.A.
- Baines, G.B.K., P.J. Beveridge and J.E. Maragos (1974): Storms and island building at Funafuti Atoll, Ellice Islands, Proc. Second Int. Coral Reef Symp. 2, Great Barrier Reef Committee, Brisbane: 485-496.
- Blumenstock, D.I. (1958): Typhoon effects upon Jaluit Atoll in the Marshall Islands. *Nature (London)*, 182: 1267-1269.
- Blumenstock, D.I. (1961): A report on typhoon effects upon Jaluit Atoll. Atoll Res. Bull. 75: 1-105.
- Blumenstock, D.I., F.R. Fosberg, and C.G. Johnson (1961): The re-survey of typhoon effects on Jaluit Atoll in the Marshall Islands. *Nature (London)*, 189: 618-620.
- David, T.W.E. and G. Sweet (1904): The geology of Funafuti. In, The Atoll of Funafuti: 61-88, London. Royal Society.
- Finckh, A.E. (1904): Biology of the reef-forming organisms at Funafuti Atoll. In, The Atoll of Funafuti: 125-150, London. Royal Society.
- Fishelson, L. (1973): Ecology of coral reefs in the Gulf of Aqaba (Red Sea) influenced by pollution. *Oecologia (Berl.)* 12: 55-67.
- Loya, Y. (1976a): Recolonization of Red Sea corals affected by natural catastrophes and man-made perturbations. *Ecology* 57(2): 278-289.
- Loya, Y. (1976b): The Red Sea coral Stylophora pistillata is an r strategist. *Nature (London)*, 259: 478-479.
- McKee, E.D. (1959): Storm sediments on a Pacific atoll. *J. Sedimentary Petrology* 29: 354-364.
- Maragos, J.E., G.B.K. Baines, and P.J. Beveridge (1973): Tropical cyclone creates a new land formation on Funafuti Atoll. *Science*, 181: 1161-1164.

- Mergner, H. (1979): Quantitative ökologische Analyse eines Riff-lagunenareals bei Aqaba (Golf von Aqaba, Rotes Meer).
Helgoländer wiss. Meeresunters. 32: 476-507.
- Mergner, H. (1981): Man-made influences on and natural changes in the settlement of the Aqaba reefs (Red Sea).
Proc. Fourth Int. Coral Reef. Symp., Manila. 1: 193-207.
- Mergner, H. and H. Schuhmacher (1981): Quantitative Analyse der Korallenbesiedlung eines Vorriffareals bei Aqaba (Rotes Meer). Helgoländer wiss. Meeresunters. 34: 337-354.
- Pearson, R.G. (1981): Recovery and Recolonization of coral reefs. Marine Ecology. Prog. Ser. 4 (1): 105-122.
- Schuhmacher, H. (1977): Initial phases in reef development, studied at artificial reef types off Eilat (Red Sea).
Helgoländer wiss. Meeresunters. 30: 40-411.
- Stoddart, D.R. (1963): Effects of Hurricane Hattie on the British Honduras reefs and cays, October 30-31, 1961.
Atoll Res. Bull. 95: 1-142.
- Stoddart, D.R. (1965): Re-survey of hurricane effects on the British Honduras Reefs and Cays. Nature (London), 207: 589-592.
- Stoddart, D.R. (1974): Post-hurricane changes on the British Honduras reefs: Re-survey of 1972. Proc. Second Int. Coral Reef Symp. 2, Great Barrier Reef Committee, Brisbane: 473-483.
- Tunncliffe, V. (1981): Breakage and propagation of the stony coral Acropora cervicornis. Proc. Natl. Acad. Sci. USA, 74 (4): 2427-2431.
- Woodley, J.D. et al. (1981): Hurricane Allen's Impact on Jamaican Coral Reefs. Science, 214: 749-755.

- Fig. 2. Approach flight to Funafuti atoll. Aerial photograph from south. Location of sections 6 and 7 below top of propeller.
- Fig. 3. Tengako Island, lagoon-side. View from SSE to Amatuku Isle (middle background) and the location of reef section 2 (middle foreground).
- Fig. 4. Funafuti Island, lagoon-side. The destroyed reef edge of reef section 3, 120 m south from the jetty of Fongafale, covered by thick layers of Dictyota bartaysii.
- Fig. 5. Fuafatu Island, lagoon-side. Inner reef at the NE-end with reef section 4. Parts of the Montipora foliosa-zone (middle) with Acropora hyacinthus (above left), Goniastrea sp.? (left) and Pocillopora eydouxi (below right).
- Fig. 6. Fuafatu Island, reef section 4. Reef flat with the well-developed Pocillopora eydouxi-zone.
- Fig. 7. Fuafatu Island, reef section 4. Crevasses in the reef flat with the Acropora hyacinthus - Pocillopora eydouxi-zone.





- Fig. 8. Fuafatu Island, SE-side. Outer reef with reef section 5. Former living reef platform with extended Montipora foliosa-crusts (middle) and dense Halimeda-stocks (above, right).
- Fig. 9. Funafuti atoll, south-end with the location of reef sections 6 and 7 (see arrows) near Tutanga Island. Aerial photograph from west.
- Fig. 10. Tutanga Island, outer reef at the SW-side. Boulder zone of reef section 6 with large boulders thrown by cyclones from western directions onto the reef flat. View from WNW.
- Fig. 11. Tutanga Island, inner reef at the SE-side with location of reef section 7 (middle right). View from NW.

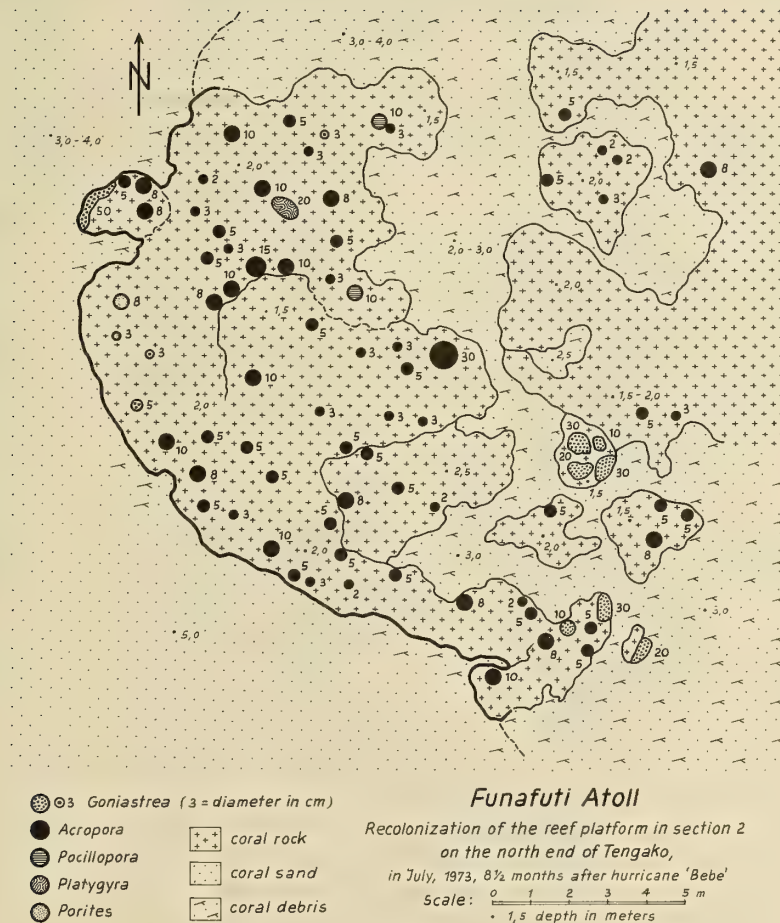


fig.13



Funafuti Atoll

Recolonization of the reef platform in section 3 near Fongafale,
in July, 1973, 8½ months after hurricane 'Bebe'

Scale: 0 1 2 3 4 5 m
• 1, 2 depth in meters

fig. 14

Table 1: Zonation and recolonization of reef section 1

Reef zone; length and depth in m	Structures and biophysiographic zones	Flora and fauna (selection); coral recolonization
Tide zone and shore channel: length 15 - 25 m, at 25 m, depth 1 m	Coral sand and coral debris on greatly cleft beach rock: Ectocarpaceae - zone	Filamentous algal lawn; aside from a few Paguridae no visible fauna
Abraded reef flat: length 110 - 150 m, depth 1 - 2 m; at 25 - 50 m: at 70 m: at 75 - 125 m: at 100 - 150 m:	Sparsely jointed abrasion zone with mud, sand and debris: <i>Chlorodesmis</i> - zone <i>Valonia</i> - zone <i>Halimeda</i> - zone <i>Caulerpa</i> - zone	Aside from some species of fish no macrobenthic fauna and only poor algal growth in biophysiographic zones: 25% <i>Chlorodesmis fastigiata</i> , single <i>Valonia ventricosa</i> , 1% <i>Halimeda opuntia</i> , 5% <i>Caulerpa racemosa occidentalis</i>
Former living reef platform: length 10 - 25 m, depth 2 - 3 m; at 135 - 160 m:	Dead coral rock flat with coral debris; single living massive corals: <i>Plesiastrea</i> - zone	A few surviving massively growing coral colonies in a zone of 25 m along the reef edge: 9 colonies of <i>Plesiastrea (versipora?)</i> and 1 of <i>Goniastrea retiformis</i> , each with 0.2 - 0.5 m Ø; no coral recolonization
Reef edge and reef slope: at 160 m, depth 4 m	Roughly cleft coral rock without preserved fine structures: <i>Caulerpa</i> - <i>Plesiastrea</i> - zone	Aside from a few species of fish no macrobenthic fauna and only 1-5% <i>Caulerpa racemosa occidentalis</i> ; no coral recolonization
Upper fore reef: from 160 - 180 m outwards, depth 4 - 6 m	Coral fine sand with plains of coral rubble	Only 7 surviving colonies of <i>Plesiastrea</i> near the reef slope, very few benthic fish species

Table 2: Zonation and recolonization of reef section 2

Reef zone; length and depth in m	Structures and biophysiographic zones	Flora and fauna (selection); coral recolonization
Tide zone and shore channel: length 5 - 10 m, depth 0.5 m	Coral sand and coral debris on greatly cleft beach rock: Ectocarpaceae - zone	Aside from a few Paguridae no visible macrobenthic fauna; filamentous algal lawn: Ectocarpaceae and others
Abraded reef flat: length 100 m, at 20-40 m, depth 1-2 m; at 50-90 m:	Sparsely jointed, largely eroded and partly muddy abrasion zone with flattened surface and small algal stocks: <i>Vasum</i> - <i>Caulerpa</i> - zone	Sparse macrobenthic mobile fauna: only 1 living <i>Conus</i> species and many <i>Vasum turbinellum</i> ; algal growth: <i>Bryopsis pennata</i> and <i>Caulerpa racemosa occidentalis</i>
Former living reef platform: length 15 - 20 m, depth 1.5 - 3 m at 120 - 140 m:	Dead coral rock flat without fine structures and mud, but roughly divided into blocks and channels with debris: <i>Acropora humilis</i> - <i>hyacinthus</i> - zone	No surviving coral colonies, but numerous resettled young colonies of <i>Acropora</i> spp., some of <i>Pocillopora</i> , <i>Porites</i> , <i>Goniastrea</i> and <i>Platygyra</i> , altogether 84 young colonies within an area of 136 m ²
Reef edge and reef slope: at 140 m, depth 3-4 m	Tabular <i>Acropora</i> - colonies overthrown by storm waves	Rich fish fauna, locally 1 hydroid species along the reef edge
Upper fore reef: from 140 m outwards, depth 3 - 5 m	Coral sand with mud and some coral rubble	More than 50 fish species: many Acanthuridae and Chaetodontidae, but no Scaridae

Table 3: Zonation and recolonization of reef section 3

Reef zone; length and depth in m	Structures and biophysiographic zones	Flora and fauna (selection); coral recolonization
Tide zone, 10 m, shore channel: length 20 m, depth 0.3 m	Coral rock blocks, muddy coral sand with rubble: Paguridae - zone	Aside from a few Paguridae only sparse macrobenthic fauna; almost no macroalgae
Abraded reef flat: length 80 - 100 m, depth 1 - 1.5 m	flattened, muddy abrasion zone, only partly visible due to algal cover, partly with coarse rubble and serious damages: Dictyota bartaysii - zone (Fig. 4)	Flourishing algal stocks: mainly <i>Dictyota bartaysii</i> , additionally <i>Caulerpa racemosa occidentalis</i> , <i>Halimeda macroloba</i> , <i>Halimeda opuntia</i> and <i>Udothea orientalis</i> ; herbivorous macrofauna: <i>Holothuria leucospilota</i> , Acanthuridae and others
Former living reef platform: length 15 - 20 m, depth 1 - 1.8 m	Largely eroded and flattened, slightly muddy coral rock area, covered to 75% with <i>Dictyota</i>	A few gastropods, some <i>Holothuria leucospilota</i> , many herbivorous fishes: Acanthuridae, Chaetodontidae, Pomacentridae (?)
Reef edge and reef slope: at 120 m, depth 3 m	Broken coral rock zone, slightly muddy without fine structures, covered to 50% with <i>Dictyota</i> ; overthrown <i>Acropora</i> spp.: <i>Acropora</i> - <i>Pocillopora</i> - zone	Sparse algal stock; no surviving coral colonies, but numerous resettled young colonies, usually <i>Acropora</i> spp. + Faviid - regenerates, altogether 67 young colonies within 50 m ² and 2.5 m breadth along the reef edge
Upper fore reef: from 120 m outwards, depth 3 - 3.5 m	Largely muddy coral sand with coral debris	Very rich fish fauna: especially Acanthuridae and Mullidae, but no Scaridae

Table 4: Zonation and recolonization of reef section 4

Reef zone; length and depth in m	Structures and biophysiographic zones	Flora and fauna (selection); coral recolonization
Tide zone: length 10-15 m	(S) Coral rubble on beach rock, (N) eroded beach rock plates	Few visible macrobenthic fauna; no macroalgae
Shore channel: length 20 m, depth 0.5 - 1 m; strong longreef current: 15 m/min.	Coral sand with fine coral debris, (S) areas of living branched corals	No macroalgae, a few fishes; (S) <i>Acropora formosa</i> - (group)
Reef flat: length 100 m, depth 1-1.5 m	Abraded coral rock flat, on it living coral zones: (S) <i>Acropora formosa</i> - zone, (M) <i>Montipora foliosa</i> - zone (Fig. 5), (N) <i>Pocillopora</i> <i>eydouxii</i> - zone (Fig. 6)	(S) dense barrier of <i>Acropora formosa</i> - (group), (M) <i>Montipora foliosa</i> , colonies up to 2 m Ø (Fig. 5), (N) dense stock of <i>Pocillopora</i> <i>eydouxii</i> (Fig. 6) with some <i>P. damicornis</i> , <i>Acropora humilis</i> and <i>Millepora dichotoma</i>
depth 1.5 - 2 m, holes up to 4 m deep	In the coral rock flat, crevasses up to 10-15 m long, varying in depth, with fine coral sand; along the rims branched corals, on the floor massive stony corals: <i>Acropora hyacinthus</i> - (<i>Pocillopora eydouxii</i>)-zone (Fig. 7)	(S) dense barrier of <i>Acropora hyacinthus</i> (Fig. 7), colonies up to 1.5 m Ø, with less <i>A. corymbosa</i> and <i>A. humilis</i> , (N) <i>Pocillopora eydouxii</i> , in the crevasses <i>Favia</i> , <i>Favites</i> , <i>Goniastrea</i> , <i>Plesiastrea</i> (<i>versipora</i> ?) and <i>Porites</i> (<i>lutea</i> ?)
Reef edge: more than 800 m away (impossible to reach)		

Table 5: Zonation and recolonization of reef section 5

Reef zone; length and depth in m	Structures and biophysiographic zones	Flora and fauna (selection); coral recolonization
Tide zone: length 10 - 20 m	Coral rubble on beach rock, (SW) beach rock plates	Aside from a few Paguridae no visible macrobenthic fauna
Abraded reef flat: length 50 - 80 m at 30 m, depth 0.5 m	Abrasion zone: sharp-edged, eroded coral rock <i>Chlorodesmis</i> - zone	<i>Chlorodesmis fastigiata</i> and <i>Lithothamnion</i> sp. Very few Pagurids and Gastropods, a few fishes
length 20 - 30 m, depth 0.3 - 0.7 m	Shingle zone: coral debris encrusted with calcareous red algae on largely eroded coral rock, few living corals: <i>Porolithon</i> - zone	<i>Lithothamnion</i> sp., <i>Porolithon</i> sp., <i>Porites lutea</i> (?), some Gastropods, a few fishes
Former living reef platform: length 20 - 40 m, depth 1 - 1.2 m	Rest of the former coral zone: living coral assemblages largely reduced by storm damages, with overthrown <i>Acropora</i> - umbrellas and green algal growth: <i>Halimeda</i> - <i>Montipora</i> - zone (Fig. 8)	Green algae: 4 <i>Halimeda</i> species (<i>H. cylindracea</i> , <i>discoidea</i> , <i>macroloba</i> , <i>opuntia</i>) and <i>Udothea orientalis</i> ; surviving corals: <i>Acropora humilis</i> and <i>hyacinthus</i> , <i>Goniastrea</i> , <i>Favia</i> , <i>Montipora foliosa</i> - crusts (Fig. 8), <i>Plesiastrea</i> (<i>versipora</i> ?), <i>Pocillopora damicornis</i> + <i>P. eydouxii</i> , <i>Millepora</i> sp.; recolonization: a few young <i>Acropora</i> - colonies
Algal ridge: length 30 m, depth 0.8 - 1 m	Typical algal ridge: minimal damage, coral rubble cemented with calcareous red algae	Aside from <i>Lithothamnion</i> and <i>Porolithon</i> no macroalgae; no living corals, a few fishes
Reef edge with the surf zone and the reef slope with its spurs and grooves 110 - 200 m away were not possible to reach due to the breakers		

Table 6 : Zonation and recolonization of reef section 6

Reef zone; length and depth in m	Structures and biophysiographic zones	Flora and fauna (selection); coral recolonization
Tide zone: length 10 - 15 m	Coral rubble, but no beach rock	Aside from a few Paguridae no visible macrobenthic fauna
Abraded reef flat: length 100 - 150 m, at 20 m, depth 0.5 - 1 m	Abrasion zone: flattened, sharp - edged eroded coral rock plain without fine sediment	No macroalgae; only a few Gastropods, crabs and fishes
at 30 m, depth 0.8 - 1.5 m	Boulder zone (Fig. 10): boulders of up to 2 m \varnothing thrown by the storm onto the coral rock	On the coral blocks only blue algae and Gastropods, single fishes beneath the blocks
at 50 - 80 m, depth 1 m rapid surface current (40 cm/s) outwards	Algal ridge: coral debris cemented with calcareous red algae: <i>Porolithon</i> - zone	No macroalgae, only <i>Porolithon</i> sp. and <i>Lithothamnion</i> sp.; aside from fishes no visible macrofauna
Reef edge at 100 m and upper fore reef: length 30 m, depth 3 - 5 m; strong surface current (30 cm/s) outwards	Reef edge largely cleft by surf erosion and settled by branched corals; spurs and grooves lead to deep canyons with plentiful live:	Outwards increasing numbers of coral colonies: 2 species of <i>Pocillopora</i> and plenty of <i>Millepora platyphylla</i> , then numerous <i>Acropora humilis</i> and <i>A. corymbosa</i> , single <i>A. hyacinthus</i> and dense barriers of <i>Millepora dichotoma</i> ; fish fauna rich in species + numbers
at depth 3 - 5 m:	<i>Pocillopora</i> - <i>Millepora</i> <i>platyphylla</i> - zone,	
at depth 5 - 10 m:	<i>Acropora corymbosa</i> - <i>A. humilis</i> - zone, <i>Millepora dichotoma</i> - zone	

Table 7: Zonation and recolonization of reef section 7

Reef zone: length and depth in m	Structures and biophysiographic zones	Flora and fauna (selection); coral recolonization
Tide zone: length 10 m	No beach rock, coarse coral rubble with sand areas	Aside from a few Paguridae nearly no visible macrobenthic fauna
Abraded reef flat: length 100-130 m, at 30 m, depth 1 m	Abrasion zone: flattened, sharp-edged, muddy coral rock	No macroalgae; only a few macrobenthic faunal species and fishes
at 40 m, depth 1-2 m	Microatoll zone: numerous microatolls cover 10-30%: <i>Porites lutea</i> - zone	Microatolls of <i>Porites lutea</i> (?) up to an height of 0.2 m, many of them dead and muddy
at 70 m, depth 2-3 m: strong surface current (25 cm/s) outwards	Single plains of coral debris between bigger microatolls: <i>Porites</i> - <i>Udothea</i> - zone	Aside from <i>Porites lutea</i> <i>Udothea orientalis</i> and <i>Lithothamnion</i> , additionally single <i>Millepora dichotoma</i> and <i>Acropora hyacinthus</i> ; a few fishes
Living reef platform: length 50-100 m, depth 3-5 m;	Pillar zone: coral rock plain with big microatolls, towards the southeast increasingly divided into pillars densely settled by living corals;	Microatolls of <i>Heliopora coerulea</i> with up to 2.5 m \varnothing and of <i>Porites lutea</i> with up to 5 m \varnothing
at 100 m, depth 3 m,	between them sand floor with mud and fine debris:	Pillars with <i>Pocillopora eydouxi</i> and <i>Millepora dichotoma</i>
at 125 m, depth 3-4 m,	<i>Heliopora</i> - <i>Porites</i> - zone,	Pillars with <i>Pocillopora</i> and some <i>Acropora</i> species (<i>corymbosa</i> , <i>formosa</i> , <i>humilis</i> and <i>hyacinthus</i> , the latter with umbrellas of up to 3 m \varnothing)
at 150-200 m, depth 4-5 m		
Reef edge: at 170-200 m; only 5-8 m of visibility	<i>Pocillopora</i> - <i>Millepora dichotoma</i> - zone, <i>Pocillopora</i> - <i>Acropora hyacinthus</i> - zone	Some <i>Conus</i> - species and <i>Tridacna</i> , only a few fish species

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STATUS AND ECOLOGY OF MARINE TURTLES
AT JOHNSTON ATOLL

By

GEORGE H. BALAZS

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STATUS AND ECOLOGY OF MARINE TURTLES AT JOHNSTON ATOLL

By

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INTRODUCTION

The aim of this paper is to consolidate all available information on marine turtles at Johnston Atoll, and to present the results of a short-term tagging study recently conducted there. The importance of this work rests on the fact that it has never been done before, that marine turtles are listed under the U.S. Endangered Species Act (since 1978), and the atoll is a National Wildlife Refuge. The Defense Nuclear Agency has operational control of Johnston with the primary mission of maintaining nuclear readiness for the resumption of atmospheric testing, should it be so directed. Several other organizations are present under Defense Nuclear Agency stewardship, including an Army chemical storage facility, a Coast Guard loran station, a NOAA weather station, and a civilian support contractor, Holmes and Narver, Inc. The U.S. Fish and Wildlife Service in Honolulu cooperatively manages the area as part of the National Wildlife Refuge System.

Johnston Atoll is located at lat. 16°45'N, long. 169°31'W, and is one of the most isolated atolls in the world. The land area consists of four islands (Johnston, Sand, Akau, and Hikina) totaling only about 2.8 km², most of which is man-made. The surrounding reef covers an area 11 by 22 km. Johnston is one of the best studied atolls in the central Pacific, due to its small size and extensive use for military purposes over the past 45 years. A comprehensive summary of the atoll's natural history, including all known scientific studies up to 1973, has been compiled by Amerson and Shelton (1976). The ecological significance of the atoll is described separately in this publication (p. 361-368) by four prominent ecologists.

Much of the previous research conducted at Johnston has been on the terrestrial fauna and flora, with major emphasis on seabirds. The studies on the marine environment and biota have been mainly centered in the lagoon. Virtually no work has been done off the south shore of Johnston Island. This has been due in part to safety and security restrictions, and poor diving conditions. Since most of the turtles found at the atoll occur in this region, it is perhaps not surprising that they have received so little attention over the years.

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The Army plans to construct a large-scale incineration facility on Johnston Island to destroy chemical agents and munitions stored there. The storage bunkers are along the south shore of the island adjacent to West Peninsula, the site where the plant will be constructed. Comprehensive information on this project, Johnston Atoll Chemical Agent Disposal System (JACADS), has been presented (U.S. Army Corps of Engineers 1983). Construction of the facility is planned to begin in late-1985, and take 3 years to complete. The number of personnel on the island will double from the present 350. Factors that have not yet been decided, or are classified for security reasons at present, include the life of the facility, the total number and kinds of munitions to be incinerated, and the disposition of certain nontoxic byproducts. Initially, at least 72,000 rockets containing 345 metric tons of nerve agent (GB and VX) are scheduled to be processed.

This paper is the culmination of work commissioned by the U.S. Army Corps of Engineers, Pacific Ocean Division, to obtain baseline data on marine turtles at Johnston Atoll. The study was prompted by the absence of information on these reptiles, their protected status under Federal law, and the proximity of the JACADS project. Recommendations given in this paper will help ensure the conservation of Johnston's turtles, as requested in the terms of reference for the study.

HISTORICAL OVERVIEW OF TURTLES

There are few accounts of sea turtles at Johnston Atoll in the literature. Amerson and Shelton (1976) summarized, as follows, all information known to them as of late 1973 (p. 112):

"Reptiles, Species Accounts - There are no general references that illustrate the reptiles of Johnston Atoll. Taxonomy of the turtles follows Carr (1972) and Amerson (1971).

"BLACK SEA TURTLE

Chelonia agassizi

"Status - Regular uncommon visitor; known from the lagoon, offshore Johnston Island, and Sand Island.

"Observations - Brooke (MS.), who visited Johnston Atoll in March 1859, commented about the lack of turtles: 'The reefs are covered with fish of various kinds. Mullet abound, but there are no turtles.' Wetmore (MS. a and b) likewise, recorded no turtles at Johnston Atoll in July 1923.

"POBSP [Pacific Ocean Biological Survey Program] personnel recorded sea turtles in the shallow marginal reef area west of Johnston Island in July 1963. An adult (USNM 163581) was collected 20 November 1966 on the beach of Sand Island. Island personnel in 1973 reported seeing 10 to 12 turtles offshore of Johnston Island throughout the year. A longtime resident estimated harvesting 12 to 15 per year.

"Annual Cycle - The Black Sea Turtle apparently visits Johnston Atoll year-round. No records exist of it breeding on the atoll, although

perhaps it did in small numbers prior to inhabitation by man. This species breeds during the summer in the northwestern Hawaiian Islands, especially at French Frigate Shoals (Amerson, 1971)."

The validity of the species account by Amerson and Shelton (1976) will be a subject of discussion later in this report.

In December 1892, Captain John Cameron of the schooner Ebon stayed at Johnston Atoll for a month after sailing directly from Laysan Island in the Northwestern Hawaiian Islands. The account of this visit (Farrell 1928) mentions sea turtles, but was not cited by Amerson and Shelton (1976). The relevant sections of Farrell (1928) are as follows (p. 402-405):

"Our first call was at Johnston or Cornwallis Island, five hundred and sixty miles south of Laysan and southwest of the eight islands of Hawaii proper. We found a good berth in its lagoon, and in a pretty little cove, on a beach of white sand, was an ideal spot for our tent. Near by were ruins of shanties built years before by a guano company; there also was a well, with pumps and pipes intact, which we cleaned and put in order.

"Signs of men, signs of shipwreck! We stumbled across two boats, both hauled above high water, one in fair condition, the other badly smashed; and in the craft were harpoons and lances and some bird shot in bags. The condition of the better boat, which was well worth the repairs I decided to give it, indicated that the men who left it there had been rescued. Else why should they have abandoned a tolerably seaworthy craft on a desert island?

"Our catches of sharks at Johnston were only fair, because our bait was principally sea birds, which the brutes did not relish as they had the flesh of hair seals; but our hauls almost filled our containers with liver oil. Now and then we took things more easily: 'Spell O!' was passed, and we hunted turtles. One of the men employed the Kusaie method of taking them by anchoring a few captive females near the beach to attract the bulls. It succeeded admirably and helped us greatly with attractive bait for shark fishing.

"We were standing to sea, bound to Fanning Island, when from the mate, who was at the masthead, came a cry of 'Sail O!' A bark under full sail was heading for us. Through the telescope we could see that she was a whaler: that was made evident by boats hanging from her davits ready for immediate use. I lost no time in pulling to her with some turtles and two pigs, welcome additions to the fare of a vessel long at sea and especially for Christmas dinner, as the day was December 24."

Votaw (1943) included some of Captain Cameron's comments about turtles in a short historical paper on Johnston Atoll. Turtles were also mentioned, but again not cited by Amerson and Shelton (1976), in a Honolulu newspaper article by Benson (1953). Describing the dynamiting necessary from 1939 to 1942 to clear out coral heads in the lagoon, Benson (1953) stated that:

"Interest was added to the process by the presence of numerous huge sharks. There was one monster in particular who demonstrated his prowess one day by swallowing a sea turtle - whole - at one gulp."

In recent years, sea turtles at Johnston Atoll have been discussed by Balazs (1978, 1980b, 1980c, 1982d). Two of these papers (Balazs 1980b, 1982d) made recommendations that stressed gathering baseline data on this little-known and isolated turtle population. A brochure describing National Wildlife Refuges in the Pacific briefly mentions that the green sea turtle is among the marine life found at Johnston (U.S. Fish and Wildlife Service, MS.).

Except for the single specimen in the U.S. National Museum listed by Amerson and Shelton (1976), there is no indication of scientific personnel having examined, tagged, or studied sea turtles at Johnston Atoll. Starting in 1978, turtle sighting report forms have been sent to resident personnel at the atoll, but only limited information could be acquired by this method (Balazs 1982d). Casual observations and counts of turtles from shore have recently been recorded in trip reports by Ludwig (1982), Ludwig et al. (1982), and Nitta (1982). Applied Eco-Tech Services (1983) included a discussion of turtle sightings in their consultancy report on water quality.

ASSESSMENT METHODS

Two field studies, totaling 28 days, were conducted at Johnston Atoll to accomplish the assessment. The first phase of study was September 29-October 13, 1983 and involved two workers. The second phase was November 3-17, 1983 involving five workers. In addition, a preliminary 2-day planning visit was made by one worker on August 30-September 1, 1983.

Capture Efforts

Efforts to capture turtles alive and unharmed were undertaken using large-mesh tangle nets, scoop nets, and scuba to facilitate capture by hand. All three of these methods have been successfully employed to study green turtles in coastal waters of the Hawaiian Islands (Balazs 1976, 1982b).

The tangle nets were made of 2-mm diameter nylon line, with a stretched mesh of 46 cm (23 cm square mesh), and a depth of 3.5 m. The length of the nets ranged from 9 to 40 m. The nets were set at the surface extending vertically through the water column. They were deployed and retrieved close to shore using a small boat at sites recommended by resident personnel, or where turtles were seen foraging or in transit. Up to five nets were set at one time at different locations. All nets were checked from land with binoculars every 1-2 h diurnally to see if a turtle had been caught.

Large scoop nets were used by approaching turtles at the surface with a boat. Efforts with scuba were directed at locating and catching turtles by hand during the course of underwater surveys.

Following their capture, turtles were taken ashore for tagging and examination for a period requiring up to 2 h. Before being released, color photographs were taken to help document morphological features.

Tagging and Body Measurements

Turtles were tagged for long-term identification with numbered Inconel² alloy tags, size 681, custom made by the National Band and Tag Company of Newport, Kentucky. Balazs (1980c, 1982a, 1983) describes the history of these tags used in Hawaii and their superior corrosion resistance compared with Monel alloy. The tags measure 25 x 9 x 8 mm, weigh 3.5 g, and are self-piercing and self-locking when applied with special applicators. Depending on the turtle's size, from two to five tags were applied to offset tag loss. Tagging sites were the trailing edges of both front flippers in the webbing between the third and fourth scales counting proximal to distal, in the axillae close to the first scale, and on a hind flipper on the inside trailing edge well under the carapace. A secondary and potentially long-lasting mark in the edge of the carapace resulted from the bone biopsy (described later).

Short-term visual recognition of tagged turtles after their release was made possible by painting a white number on each side of the carapace using Dupont Lucite spray paint. Based on studies elsewhere, it was estimated that these numbers would remain visible for at least 10 days.

Observations on the turtles consisted of: straight-line (SCL) and curved (CCL) carapace length from the center of the precentral scute to the posterior tip of a postcentral scute; straight-line carapace length from the center of the precentral to the notch between the postcentrals; straight-line and curved carapace width at the widest point (the sixth marginal scute); straight-line plastron length along the midline; straight-line head width at the widest point; tail length from the posterior rigid edge of the plastron to the tip of the tail; straight-line flipper width from the claw scale to the sixth scale on the trailing edge; and body weight.

Food Sources and Epizootics

Food sources were determined by sampling the turtles' stomachs with a plastic tube inserted through the esophagus. Small amounts of water were introduced and aspirated to obtain food material. In addition, unswallowed particles of food were removed from the mouth, and fecal material that could be collected was rinsed to isolate incompletely digested food. These three field techniques for sampling dietary components are discussed in detail in Balazs (1980a). Observations made of turtles feeding at specific sites also permitted the direct collection of algal forage during underwater surveys.

²Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Food items were preserved in dilute Formalin and identified to the lowest taxon possible. Frozen bulk samples collected from the foraging habitat were biochemically analyzed to determine major nutrients and mineral composition.

Epizootes found on the skin and hard parts of the turtles were scraped off, preserved in dilute Formalin, and identified to the lowest taxon possible.

Biopsies and Blood Sampling

Biopsies of bone and lamina were taken with a saw by cutting a small triangular piece from the edge of the 10th left marginal scute. Depot fat was sampled from directly under the skin by making a 2-3 cm incision in the inguinal region. Tissue sampling procedures described by Rainey (1981) and Menzies et al. (1983) were used as a guide for this work. Bone and fat samples were frozen in glass vials and stored for future analyses of radio-nuclides and heavy metals.

Blood collection followed the methods described by Owens and Ruiz (1980) and Bentley and Dunbar-Cooper (1980). A needle and syringe were used to draw blood from the paravertebral sinus on either side of the midline of the dorsal neck surface. The blood was centrifuged and separated into packed cells and serum. Sera were frozen and analyzed for testosterone levels to determine sex. Packed cells were refrigerated and analyzed within a few hours for cholinesterase activity. The 17-Minute Manual Method, routinely used at the Johnston Island medical facility to detect anticholinesterase intoxication in humans, was used for analysis of turtle blood.

Underwater Surveys

Underwater scuba surveys were made to census turtles, locate and assess prominent foraging and resting habitat, and gather other ecological data. Two or three divers working together within visual range carried out the surveys. All surveys took place during the daytime.

Terrestrial Surveys

Terrestrial surveys were conducted along the coastlines of all four islands for the purpose of locating possible nesting and basking habitat. Systematic observations from shore were also made of coastal waters.

Personal Interviews

To compile anecdotal information, fishermen and divers, especially those who have been at Johnston for many years, were interviewed. Requests were also made to examine photographs in private collections showing turtles caught during past years.

Literature Search

The published and unpublished literature pertinent to Johnston Atoll was reviewed. This search included articles in the two major Honolulu newspapers. All known historical reference to turtles at the atoll have been presented in the previous section of this report. However, the literature review also encompassed articles on perturbations to the environment that could be of significance to turtles or their habitat.

An inquiry was made to the U.S. National Museum (Washington, D.C.) to obtain further data on the specimen mentioned by Amerson and Shelton (1976) as having been collected in 1966 "...on the beach of Sand Island."

FINDINGS

Results of Capture Efforts

A total of 21 turtles were captured (Table 1). All were green turtle, Chelonia mydas, taken with nets, and no repeat captures were made. There were no scars indicative of old tags being shed. No turtles were caught with scoop nets or by hand, due mostly to turbid water conditions and the rapid diving behavior of the turtles when approached by boat. The locations selected for the nets were exclusively off the south shore of Johnston Island (Fig. 1). Nearly all of the turtles sighted during the surveys were in this area. The high concentration along this side of the island was also confirmed by everyone interviewed. The water off the south shore is silt-laden resulting in poor underwater visibility. Reasonably good water clarity was found at other sites in the atoll.

The daily netting effort at each location, expressed in meter-hours (MH) (length of net by hours fished), is shown in Table 2. During phase 1 of the field study, nets were regularly set at locations 1-5 and left both day and night. However, this sampling procedure proved unworkable because of the high incidental capture of eagle ray, Aetobatus narinari, and large manta ray, Manta birostris. The entanglement of rays occurred only at night or during twilight hours. Once caught, manta rays were able to twist with such force that sections of the net became snarled and useless. Eagle rays caused less of a problem, but were still able to pull sections of floatline underwater and hold them there. Most turtles caught with rays under these conditions would have drowned. During the times the nets were left out at night, only one turtle was caught, apparently at morning twilight (Table 3, tag No. 7451). Although eagle rays were also in the net, the turtle escaped injury due to its large size and place of entanglement away from the rays. All netting during phase 2 was conducted diurnally (Table 2) to eliminate the problem of accidentally catching rays. Shore observations during the daytime indicated that at least some turtles avoided the nets. Avoidance would probably not have been possible at night.

Nets were set at 17 sites, but turtles were caught at only 4 of them (Table 1). Three of these locations (1, 2, and 3) were close to or immediately east of the West Peninsula, and one location (7) was between West Peninsula and the southwest corner of the island (Fig. 1). Eight of

the 21 turtles were caught at location 2; 5 each were caught at locations 1 and 7; and 3 were caught at location 3. Catch per unit effort was considerably better at locations 2 and 7 (589 and 550 MH per turtle, respectively; Table 1). A similar catch per unit effort was obtained during phase 1 and phase 2 field studies (1,123 and 1,197 MH), although twice as many turtles were caught during phase 2 (14 versus 7).

Species Present

The turtles captured displayed no clear characteristics that would justify their designation as C. agassizi, the black turtle of the east Pacific. The large size of the adults, the contour of the carapace, and the color of the plastron were all mostly consistent with C. mydas. An exception was a specimen that had a strongly tapered posterior to the carapace, and a moderate amount of gray pigment in the ventral surface of the marginal and postcentral scutes (tag No. 7551). These features are pronounced in C. agassizi, including dark pigment throughout much of the plastron. This turtle therefore seems to be intermediate between agassizi and mydas. None of the other turtles captured, nor those remembered by Cris Balubar, a resident employee and former turtle fisherman, had dark pigment in the plastron.

Carapace color and pattern varied considerably, ranging from predominantly tan with brown radiations (tag No. 7451) to olive with black flecks (tag No. 7517). When seen in the water before capture, the carapace of most turtles at Johnston is masked by a layer of silt. Carapace coloration within other green turtle populations, such as in Hawaii, is known to vary with stage of maturity, sex, and possibly even environmental factors (Balazs 1980c). However, the carapace and dorsal skin surface of adult C. agassizi is always predominantly black.

The observation by Amerson and Shelton (1976) that the black turtle occurs at Johnston is invalid based on findings of this present study. Amerson and Shelton's (1976) nomenclature appears to have been founded almost completely on their citation of Carr (1972), who stated (p. 25):

"...The black turtle of the eastern Pacific lacks the numbers to withstand that abuse, and may well become an incidental casualty along the American mainland shores. To my eye, however, the black turtle stock occurs elsewhere--in the Galapagos Islands, among the mid-Pacific Islands, and in parts of the Indian Ocean. With its range extending through so much territory, the complete loss of the Mexican and Central American colonies might not obliterate Chelonia agassizi; but here again, the name, as I am using it, surely covers a number of hitherto unnamed races. The sooner these are properly defined, the sooner concern over their plight will be generated."

No other species of sea turtle was seen during the field studies. An unverified sighting of a hawksbill turtle, Eretmochelys imbricata, is listed by the U.S. Army Corps of Engineers (1983). In addition, four turtles, thought to be hawksbills, were reported in shallow water off the northeast corner of Johnston Island in September 1980 (R. J. Novak in

litt. to G. H. Balazs). Cris Balubar and others interviewed indicated that only green turtles have ever been seen by them within the atoll.

The leatherback turtle, Dermochelys coriacea, has been observed on several occasions by personnel trolling for fish outside the atoll. Cris Balubar saw one about 11 km to the north of the atoll. In 1981, a large decapitated (but still moving) leatherback was seen, apparently after being accidentally hit by a boat. Efforts to gaff the turtle and bring it aboard proved unsuccessful.

Population Structure

Body measurements and weights presented in Tables 3, 4, and 5 indicate that 60% (14) of the turtles captured were mature adults. Turtles <82.9 cm SCL were estimated to be immature (see Balazs 1980c for a discussion of size categories). The proportion of adults in the Johnston population is therefore substantially greater than at coastal areas studied in Hawaii. At a comparable foraging area on Molokai, Hawaii only 9% of 81 green turtles sampled with nets were adults. The sighting of turtles during surveys at Johnston, along with information resulting from interviews, confirmed that the population is composed of mostly large turtles. The smallest turtle captured was 57.4 cm SCL; however, a few others estimated to range down to 35 cm SCL were seen during the surveys.

The age structure and growth rates of turtles at Johnston are presently unknown. In the Hawaiian Islands, green turtles are estimated to take 11-59 years to grow to an adult. Growth rates have been found to differ significantly among resident foraging areas within the archipelago (Balazs 1982b). The high percentage of adults at Johnston could be caused by several factors, including rapid growth rates, low recruitment of small turtles to the population, high predation and mortality of small turtles, and low predation and mortality of adults.

The 15 turtles that were weighed ranged from 63.6 to 151.4 kg (Table 5). The mean weight of three adult males was 104.8 kg (range 84.5-115.9 kg). The mean weight of six adult females was 112.0 kg (range 87.7-115.4 kg). The largest turtle ever caught by Cris Balubar was a 186 kg male.

Testosterone levels were determined from blood samples of 12 turtles for sex determination. The sex of six other turtles, all adults, could be determined by external features (i.e., a long, large tail for males). The sex ratio of this 18-turtle sample was 2.6:1 in favor of females (Table 6). If only immature turtles are considered, the ratio was still 3:1 in favor of females. Of special interest among the immature turtles was a fairly large specimen (79.1 cm SCL, 74.1 kg) that still had a short tail (18.2 cm). The testosterone level showed this turtle to be a male.

Abundance and Distribution

Capture and tagging efforts were focused at principal aggregation sites of turtles. Seven turtles were tagged during phase 1 from this area. After an interval of 20 days, phase 2 capture efforts yielded 14

more turtles, none of which had been tagged earlier. Because no recaptures were made, these data alone do not permit an estimate of the number of turtles present along Johnston Island's south shore.

Only one paint-marked turtle was resighted. This turtle was observed at the surface near dive location I (Fig. 2) by a resident employee sailing a Hobie cat. The turtle dove vigorously when approached. Turtles have been occasionally seen in this general area, which consists of a dredged turning basin and ship channel along the eastern portion of Johnston Island's north shore. This turtle (tag No. 7485), had been captured 6 days earlier on November 6 at net location 2, and released shortly thereafter at the port facility on the north shore (Fig. 1). All 7 turtles captured during phase 1 and 12 caught during phase 2, were released at this site. The other two turtles (tag No. 7560 and 7565) from phase 2 were transported by truck and released at the south shore. The short distance (2 km) around the island, in relatively calm water between the north and south shores, should not have presented an obstacle to the turtles. Biotelemetry has shown that immature green turtle have a well-developed homing ability on their resident habitat (Ireland 1979a, 1979b). Furthermore, adults can find their way across hundreds of kilometers of ocean when migrating between resident areas and nesting beaches (Hirth 1971; Carr 1972).

Only three turtles were seen during 26 diving surveys with scuba totaling over 22 h, or 46 man-h, of bottom time (Fig. 2). All three turtles were swimming when sighted. While it was not possible to approach close enough to capture them, the turtles nevertheless did not flee in the manner seen when encountered by boat at the surface. The turtles were sighted at dive locations D, J, and P off the south shore in the same general area where nets were set. Most of the dive surveys (18 of 26) were made here, but poor underwater visibility, ranging from at best 10 m to as low as 1.5 m, greatly limited the possibility of seeing swimming turtles. However, careful systematic searches of the bottom were made at all locations to find places where turtles were sleeping, hence less liable to flee from a diver. None was found, although most areas surveyed, from just several meters offshore out to 1.8 km (dive location U), appeared well suited as sleeping habitat. Sleeping sites repeatedly used by green turtles have recognizable marks in the substrate. Except for two possible minor sites at dive locations C and P, no habitat was found showing such usage. The major sleeping areas for turtles along the south shore remain undiscovered, but it seems unlikely they are commuting very far.

As shown in Figure 2, no diving surveys were made to the southwest of West Peninsula in the waters downwind of the sewer outfall. In addition to raw human sewage, the outfall discharges wash water from the decontamination procedure used at the chemical storage facility. Other effluent, a dense black discharge, was regularly seen from shore during phase 1. This was reported to result from flushing of old sewer lines. The discharge point of the sewer outfall is immediately southwest of dive location J (Fig. 2). No turtles have been seen underwater during the few dive surveys previously made downwind of the outfall (Ludwig et al. 1982; Applied Eco-Tech Services 1983). However, from shore, turtles are commonly seen

in this area while at the surface. It is possible that the sleeping areas are located somewhere along here. Recreational swimming and scuba diving are not permitted in waters off the entire south shore of Johnston Island.

Sightings of individual turtles at the surface, other than along Johnston's south shore, were made once at dive location O, and four times in the ship channel at the east end of Johnston Island. In addition, three immature turtles were seen over the tops of coral heads in the vicinity of dive location X. No turtles were seen in coastal waters by observers placed on Akau and Hikina Islands from 0800 to 1700 on November 10, and at Sand Island from 0800 to 1700 on November 11. No turtles were seen during snorkel surveys made by two observers for 80 min on November 9 in shallow water off the east and north end of Sand Island. No turtles were seen by two observers during 30 min of observation on October 12 from the abandoned tower near dive location L. These findings, which suggest low numbers of turtles and sparse distribution at sites other than Johnston's south shore, are consistent with information gathered during interviews. For example, Armyman Tim Snover stated that, over the past 10-month period, he had never seen a turtle during six scuba and eight snorkel dives in the northern portion of the atoll at Donovan's Reef (Fig. 2). Other personnel have seen turtles there, but only occasionally.

The reports of turtles in abundance along Johnston's south shore, and especially off West Peninsula, contrast sharply with the low numbers seen elsewhere in the atoll. For example, Ludwig (1982) saw an estimated 30 turtles during 1 h of observation from West Peninsula at 1800 on September 15, 1981. Up to five at a time were seen around the tops of individual coral heads. When Ludwig (1982) visited here again on September 17, he spotted eight turtles during 30 min. Ludwig (1982) also reported that personnel frequently visit West Peninsula to watch turtles. During 3 days in July 1982, Nitta (1982) saw 8-11 turtles while viewing from West Peninsula in the late afternoon. Applied Eco-Tech Services (1983) made the following comments from surveys conducted along the south shore during June 2-11, 1983.

"Although the survey team was not directing their efforts to turtle observations, nearly every head bearing Bryopsis was seen to have one to perhaps four specimens of Chelonia mydas in the immediate vicinity....Upon sighting the dive boat, these turtles would sound rapidly, move away from the area and resurface 20-40 m away. This behavior and the uncertainty of the general movements of the turtle population during the course of the day precludes an accurate estimate of the total number of turtles present off the south shore at any given time. The algae survey team typically noted 20-25 turtles during each morning's efforts (3 h) and a similar number during each afternoon. It should also be noted here that this estimate is conservative since it represents sightings of surfacing animals only, the water clarity being sufficiently poor to prevent sightings of submerged organisms."

At the beginning of phase 1, four to six turtles were commonly sighted off West Peninsula, usually within a few hours of high tide. However, the number spotted varied considerably (0-13) while motoring

along the entire south shore at various times throughout the study. These counts were undoubtedly influenced by tide stage, changes in visibility due to sun angle, and probably a greater awareness by the turtles of an approaching boat. At the end of phase 2, on November 16, an observer was stationed at West Peninsula for an hour during an incoming high tide. No fewer than five and possibly as many as eight turtles were seen; none of which appeared to have painted numbers. These data suggest there may be a considerable turnover in turtles using the area, and that the total number may be many times larger than what can be seen during a several day period.

Food Sources

Samples of stomach contents, mouth contents, or feces were acquired from 13 of the 21 turtles captured. Stomach contents from eight turtles contained five kinds of benthic algae, diatoms, filamentous bacteria, unidentified fibers, and a single amphipod (Table 7). The green algae, Bryopsis pennata var. secunda, was prominent in samples from three turtles and Caulerpa racemosa var. uvifera prominent from one turtle. All other items were present only in relatively small or trace amounts. Mouth contents from five turtles contained five kinds of benthic algae (including unidentified blue-green algae), diatoms and a single amphipod (Table 8). A stomach sample had already been taken from one of these turtles and the mouth contents were identical. Of the four turtles sampled only for mouth contents, B. pennata var. secunda was prominent from two C. racemosa var. macrophyssa prominent from the other two. Identification of fecal contents from the single turtle sampled revealed a composition of 75% C. racemosa var. uvifera, and 25% B. pennata var. secunda (Table 8). Differences in the digestibility of the two species could have affected these percentages, therefore, the actual ratio ingested is unknown. Based on the limited sample data presented for stomach, mouth and fecal contents, the size of the turtle does not appear to be a factor in the kind of alga eaten. The turtles' major food sources (Bryopsis and two varieties of Caulerpa) grow in prime foraging habitat near the West Peninsula. Turtles were commonly seen surfacing and diving in typical foraging behavior over coral heads having dense Bryopsis. Interestingly, Bryopsis is not among the 56 known species of algae used as food by Hawaiian green turtles, nor has it been recorded anywhere else as green turtle forage. However, C. racemosa is eaten at several locations, but seems to be poor forage yielding very slow growth rates in green turtles (Balazs 1980c, 1982b).

Cris Balubar stated that the turtles he recalls cutting open and cleaning only contained the two common types of seaweed (Caulerpa and Bryopsis) found along the south shore of Johnston Island.

An unidentified cuboidal jellyfish (Cubomedusae) was abundant along Johnston's south shore during the early part of phase 1. The bell of these animals measured about 13 cm long. Many of them settled into the numerous depressions between coral heads where torn pieces of Bryopsis also collected. No evidence was found that green turtles feed on these jellyfish. However, other hydrozoans, such as Physalia and Velella, are eaten on an opportunistic basis by green turtles in Hawaii (Balazs 1980c).

Kitchen waste is dumped into the ocean daily at the southwest corner of Johnston Island. Pritchard (1982) reports that some green turtles scavenge regularly for food scraps discarded in a similar manner at the military facility on Kwajalein Atoll. No evidence was found that this food source is utilized by turtles at Johnston.

The circumstances in which a fecal sample was collected from a turtle (Table 8) are of interest. This turtle was captured at net location 7 at 1700 h on November 8 along with another turtle (Table 3). A section of the net had become snagged on a nearby coral head, thus preventing it from reaching the surface to breathe. The turtle was comatose when recovered. Except for contraction of the tail when pulled straight, there were no signs of life. Periodic compression of the plastron for 1 h in an attempt to ventilate the lungs gave no apparent results. The movement of air by this method seemed to only take place through the esophagus, since the glottis remained tightly closed. A small diameter plastic tube was therefore pushed through the glottis to hold it open and afford passage of air. The lungs were then gently ventilated by blowing into them at irregular intervals for the next hour with the turtle in a prone position. The turtle raised its head and opened its mouth to breathe for the first time after being seemingly lifeless for over 2 h. The tube was removed as breathing gradually became more frequent, and movement of the flippers resumed. The turtle was subsequently left prone overnight to give it more time to recover before release. In the morning, 1.5 kg of fecal matter were found to have been passed. The turtle swam off and dove in a normal manner when released.

Foraging Habitat

The principal foraging habitat for turtles at Johnston Atoll consists of a narrow band of heterogeneous algal pasture immediately off and along the south shore of Johnston Island. To a lesser extent, this feeding zone also exists contiguously on the northeast side of the ship channel (dive location X, Fig. 2), where *Bryopsis* alone is present on the tops of coral heads. Based on published literature, personal interviews, and surveys conducted during the present study, the standing crop densities of benthic algae suitable as forage for green turtles are extremely low at most all other sites in the atoll. Many kinds of benthic algae occur at Johnston (Brock et al. 1966, Buggeln and Tsuda 1966, 1969; summarized by Amerson and Shelton 1976). From this literature, Balazs (1982d) previously noted that *C. racemosa*, *Codium arabicum*, and *Gelidium pusillum* might serve as algal forage for Johnston's turtles, since green turtles elsewhere feed on these three species. However, the apparently sparse quantities of the latter two species negate any significant benefit that could be derived. There are small areas of *Caulerpa racemosa* var. *uvifera* in shallow water around Sand, Hikina, and also possibly Akau Island that could be used by turtles, but no turtles were seen feeding at these locations.

Four kinds of benthic algae collected during diving surveys along Johnston's south shore comprise nearly all of the standing crop that exists there (Table 9, dive location J). Three of these, *B. pennata* var. *secunda*, *C. racemosa* var. *macrophyssa*, and *C. racemosa* var. *uvifera*, were identified as major food sources from the stomach, mouth, and feces

of turtles. The fourth alga, C. serrulata (Förskal), was commonly seen in many areas close to the south shore, often growing in proximity to the two varieties of C. racemosa. Since C. serrulata was not found in any of the food samples, the turtles must be actively ignoring this species. Such an aversion could be due to metabolites known to be present in some Caulerpa that can act as toxic feeding deterrents (Paul and Fenical 1982; Paul 1983). This deterrence has not been demonstrated in turtles, but the subject warrants investigation. Certain algae of the Order Caulerpales are food sources for green turtles at a number of locations worldwide. More than 100 species are known, and at some atolls in the Pacific very dense populations of the algae are present (Meinesz et al. 1981).

Bryopsis and the two varieties of C. racemosa sampled fresh from foraging habitat off West Peninsula were found to differ considerably in nutrient composition (Table 10). Bryopsis contains 2 to 3 times as much protein as Caulerpa, and only about 60% the ash content. Bryopsis also has 2 to 4 times greater lipid content (ether extract). It should be noted that the protein percentages shown in Table 10 were obtained by a standard analytical procedure used for terrestrial forage (proximate analysis), where total nitrogen is multiplied by a value of 6.25. This may be an overestimate for certain marine benthic algae. For example, Dawes and Goddard (1978) measured protein in C. racemosa (variety not stated) from Florida by a direct protein extraction technique that gave a content of 4.8%. Protein content for racemosa in the present study was calculated to be 8.0% (for uvifera) and 9.1% (for macrophyssa).

The nutrient composition of Bryopsis collected from two different environments is also presented in Table 10. In one, Bryopsis was sampled off the top of a coral head where turtles were commonly seen feeding. The other collection was made nearby from a depression between coral heads where drifts of naturally torn Bryopsis had collected due to low water movement. Bryopsis in these depressions is not visible from the surface due to high turbidity. Consequently, it is unknown if turtles ever feed on this loose material. It was theorized that attached Bryopsis repeatedly cropped by turtles might contain higher protein and less fiber (complex polysaccharides) due to the constant new growth taking place at the grazed ends. Protein levels shown in Table 10 do not support this hypothesis, since the loose material is almost 2% higher (25.7% versus 23.8%) in protein content than the attached alga. However, attached Bryopsis is slightly lower in all the fiber components. It is worth noting that the drifts of loose Bryopsis can probably remain healthy and unattached indefinitely, so long as nutrients are sufficient, and currents weak enough, to prevent the drifts from being washed away (D. J. Russell, pers. commun., December 1983).

The mineral composition determined for the two different collections of Bryopsis is very similar (Table 11). The one prominent value for the nine minerals measured in these algae is the iron content of C. racemosa var. macrophyssa (2,558 ppm). This level is many times higher than that of the uvifera variety (90 ppm) or either sample of Bryopsis (88 and 110 ppm). No firm explanation can be offered for these data. However, it is possible that macrophyssa has a high requirement for iron, which therefore may be a limiting nutrient to growth. Iron pilings and pipes along the south shore

of Johnston may supply this nutrient and allow the alga to proliferate as it does. This explanation is supported in part by data discussed in Russell and Carlson (1978) concerning shipwrecks and the concomitant vigorous growth of certain green algae.

Surveys to characterize and define the habitat limits for the different algae comprising the turtle foraging zone along the south shore resulted in the following findings. The occurrence of attached Bryopsis is confined almost entirely to the tops of coral heads that range from not more than 2 m beneath the surface, to those that are fully exposed at low tide. This environmental range appears to be a necessity for lush Bryopsis growth off the south shore. Only a limited number of coral heads fulfill the requirement. Many of the Bryopsis covered heads have growth 1-2 m down their slope, but thereafter the alga is sparse. A few small patches of attached Bryopsis were found on the sides of some heads as deep as 7.5 m.

The number of coral heads with Bryopsis was censused off the south shore at low tide from a boat on November 16. Between East Peninsula and the row of iron pilings (Fig. 1), 30 individual heads were counted, as well as a narrow broken ridge in shallow water parallel to shore. Between the iron pilings and the southwest side of West Peninsula, 31 heads were counted. From West Peninsula to the southwest corner of the island, 18 were counted. A total of only about 80 heads therefore occur in this narrow zone, and most (62) are between East and West Peninsulas. The greatest distance of any coral head from shore is about 600 m. Six of the heads that were believed to be representative of all the various sizes were selected and measured to determine vertical surface area where Bryopsis occurs. The heads were irregular and difficult to measure. Nevertheless, the areas ranged from approximately 9 to 127 m²; the mean was 47 m². An "average" size coral head hosting Bryopsis is therefore only about 7 x 7 m. It was estimated that Bryopsis covered 80% of the surface area, the remainder being bare coral rock. This surface coverage could very well change with season. The distribution of Bryopsis off Johnston's south shore as portrayed in a map prepared by Applied Eco-Tech Services (1983: Fig. 24) greatly overrepresents the habitat area where this alga actually occurs.

As previously mentioned, there are coral heads to the northeast of East Peninsula where environmental conditions are conducive to Bryopsis growth and turtles were seen feeding. This area was not as thoroughly surveyed. There are probably not more than 15 coral heads there that host Bryopsis.

Turtles foraging on the tops of coral heads with Bryopsis are highly visible due to the shallow depth, and the contrasting color of the turtle's silty-brown shell against the green-black mat of Bryopsis. Because turtles are so apparent when foraging at these sites, it was possible to ascertain that some heads were being used more heavily than others. Cris Balubar also confirmed this point. For many heads, it is essential for the tide to be high enough for turtles to swim over the top to forage. At

a few sites, this condition is never met. Two prominent coral heads off West Peninsula, are emergent much of the time, and even at high tide waves break with sufficient force to prevent turtles from feeding on top.

The growth of Caulerpa in the foraging habitat along Johnston's south shore is more difficult to characterize and define because, unlike Bryopsis, most of it cannot be seen from the surface. The extensive diving surveys with scuba devoted to examining habitat between the East and West Peninsulas helped to elucidate Caulerpa distribution. The macrophyssa variety was far more abundant than uvifera or serrulata. The greatest Caulerpa coverage, approaching 100% on all hard substrate, occurred between the iron pilings and West Peninsula. Drifts of loose Caulerpa (again mostly macrophyssa) covered nearly all of the silt bottom areas between the pinnacles and other hard substrate. There was a considerable decline in Caulerpa growth seaward from the outer iron pilings and the end of West Peninsula. At a point <100 m from the end of West Peninsula, in the area of net location 2 (Fig. 1), the growth of Caulerpa nearly disappears. Throughout this transition zone, the Caulerpa coverage declines first on the seaward sides of the underwater pinnacles. With the disappearance of Caulerpa, the hard substrate consists of bare rock, an increasing amount of live corals, and the Bryopsis previously described. A consistent salinity of 34‰ was recorded from nine water samples taken throughout the area, including one taken at the greatest bottom depth of 8 m. The seawater temperature ranged from 27.5° to 28.5°C.

The findings in this study relating to Caulerpa coverage between the iron pilings and West Peninsula are considerably different from those presented by Applied Eco-Tech Services (1983). Figure 23 in their report shows 80% to 100% coverage of Caulerpa on hard bottom substrate extending 200 m seaward of West Peninsula, twice the distance described in the present report. Possibly there was a radical seasonal change, since the survey by Applied Eco-Tech Services (1983) was done in June 1983, 5 months before the present study. Confirmation of this important point is needed.

The history of the marine environment off Johnston's south shore is virtually unknown due to the paucity of research conducted there. Sections of marine habitat have been filled in with the island's periodic expansion. When Cris Balubar arrived in 1962, he recalls many turtles being present off the south shore, along with clear water and "nice reefs." He does not remember the status of algal cover. Lee Gohr helped to lay the existing sewer outfall in 1964 and recalls seeing benthic algae, but not in the density that exists at present. None of the personnel interviewed was able to tell where the outfall existed before 1964.

The exact role of sewage discharge in facilitating, or possibly depressing, algal growth remains speculative. Aerial photographs of the island taken over the years may help to answer this question. It may be that nutrients from guano in the brackish-water lens of the island historically served as fertilizers for algae.

Epizootics and Abnormalities

Epizootic algal mats found mostly on the inguinal skin, plastron, and ventral surface of marginal scutes were sampled from five of the turtles captured. An analysis of this material revealed eight kinds of algae, roundworms, foraminifera, amphipods, and black "mites" (Table 12). One of the algal species (Pilina sp.) may possibly be a new record for the tropical Pacific. The red alga, Polysiphonia tsudana, was present on all five turtles, and is also common on Hawaiian green turtles. Acrochaetium, Sphacelaria, and Lygbya have also been recorded on green turtles in Hawaii, but for the latter two genera as different species. Urospora sp., found on three turtles, has never been reported from turtles in Hawaii. Amphipods found on two turtles and in the mouth and esophagus of another turtle are probably Hyachelia tortugae (Tables 7 and 8). This specialized crustacean, first described from the Galapagos Islands, has also been recorded in Hawaii and is known only from sea turtles.

There was a noticeable paucity of barnacles on the turtles captured. None of the common turtle barnacle, Chelonibia testudinaria, was present, nor was the burrowing barnacle, Stephanolepas muricata. Even more surprising was the near absence of the harmless skin barnacle, Platylepas hexastylus. Only a few were found on two turtles and some of these were falling off and appeared to be dying. Platylepas commonly occurs in large numbers on the skin of Hawaiian green turtles.

Small neoplastic growths 1-3 cm in diameter were found on two male turtles captured. Five growths were present on one and two on the other. The sites of these tumors included the trailing edge of front flippers, corner of the mouth, edge of the eye, inguinal region, and top of the head. Except for the latter location, growths are occasionally seen at these same places in Hawaiian and other green turtle populations. Some of the tumors documented elsewhere have been much larger, and far more numerous on individual turtles, than the ones seen at Johnston. However, Cris Balubar reported that about 10 years ago he did see a turtle "covered with white growths." The etiology of tumors on sea turtles is presently unknown. Relevant background material on the subject can be found in Harshbarger (1977), Balazs (1980c), Glazebrook et al. (1981), Jacobson (1981), and the references contained therein.

Counts made of the major scales along the trailing edge of the front flippers, to a point perpendicular to the claw scale, revealed that 2 (9.5%) of the 21 turtles varied from the standard 6 left-6 right count (Table 5).

The number of postocular scales (scales posterior of the orbits) varied from the standard 4 left-4 right count in 4 (19%) of the turtles (Table 5).

Four other abnormalities were noted among the turtles captured. The tail of an adult female was curled tightly under the edge of the carapace and appeared to be paralyzed. There was no scarring to suggest an injury.

One turtle made an unusual "whistling" sound when breathing. The cause could not be determined. Another had a small extra scute along the midline of the plastron between the humeral scutes, and another had a slightly depressed area to the carapace in the region of the 2d central scute and 1st-2d right lateral scutes. There were no signs of an external injury.

Predation and Injuries

Evidence of injuries likely resulting from shark attack was seen on 3 of the 21 turtles captured. The injury on an adult male was the most pronounced: half of its tail was amputated and it had extensive, but mostly healed, lacerations of the right hind flipper. Two turtles had several deep cuts in their carapace. Some of these wounds, which were also mostly healed, could be seen near the painted numbers. Five other turtles had minor pieces missing from hind flippers, but this is common in green turtles. None of the turtles in Cris Balubar's photos showed signs of shark attack or other obvious injuries. The few probable shark-inflicted injuries seen at Johnston may not necessarily have happened there, since the adult turtles must periodically migrate elsewhere for breeding purposes.

Sea turtles are known to be prey for large sharks, especially the tiger shark, Galeocerdo cuvier. Captain Cameron was well aware of this food preference when he used turtles as bait to enhance his shark fishing at Johnston in 1892 (Farrell 1928). The graphic description by Benson (1953) of a shark swallowing a turtle whole at Johnston also attests to this fact. More recently, C. B. Cechle, in litt. 1979 cited by Balazs (1982d), reported sharks feeding on a large turtle outside of the atoll.

Tiger sharks presently occur at the atoll, but they are not commonly seen nor frequently captured in recreational shark fishing. The most recent one caught was in August 1983 when a 4-m specimen was hooked in the ship channel at the western end of Sand Island. A 1-m whitetip reef shark, Triaenodon obesus, was used as bait. The stomach was not cut open, so the natural prey items are unknown.

The gray reef shark, Carcharhinus amblyrhynchos, often schools in abundance off the southwest corner of Johnston Island when kitchen garbage is dumped. Recreational fishermen fish for shark with baited hooks from shore here and at West and East Peninsulas. However, no reports were received of turtle parts ever being found in the stomach of gray reef sharks. Elsewhere this species is apparently not a regular predator of turtles, except possibly on hatchlings. One person interviewed stated that he had seen two turtles feeding on dead fish used as bait on a shark hook at West Peninsula.

Fishing for large tiger sharks used to be done with baited hooks set from markers along the main ship channel. This practice became prohibited, so personnel moored two large iron buoys 200-300 m offshore between West Peninsula and the southwest corner of the island. Both buoys are still present, but not often used for fishing since only small sharks (presumably gray reefs) have been caught there. During the diving surveys, only two

sharks were seen, a gray reef at location M, and a whitetip at location L (Fig. 2). Large numbers of the former are said to enter the atoll for breeding purposes during the summer months.

The moray eel, Lycodontis javanicus (= Gymnothorax), occurs at Johnston Atoll where it is known to be an opportunistic predator of fish, octopus, and spiny lobsters (Brock 1972). This species is the largest moray eel in the Indo-Pacific; specimens seen at Johnston are estimated at up to 2.4 m long (Randall 1980). Lycodontis javanicus could conceivably prey on small immature green turtles, but there is no direct evidence showing this. However, a prey item as large (and unusual) as a 46.5 cm whitetip shark was found by Brock (1972) in the stomach of a 1.4 m moray eel. Eels live under ledges and in other coral recesses similar to where green turtles are typically believed to sleep. The eel's abundance and prey items have not been intensively studied along the south shore of Johnston Island. None was seen during any of the diving surveys. However, moray eels hide mostly in the reef during the daytime, and feed during twilight and at night.

Large groupers (Serranidae) occur at Johnston, but there is presently no evidence that they prey on turtles. In Hawaii, and elsewhere, whole immature turtles have occasionally been found in the stomachs of these fish. Benson (1953) describes the capture of a stunned "430 lb (195 kg) black sea bass" following an explosion to clear coral in the lagoon. The contents of the stomach were not mentioned. Sometime during 1970-71, a 27 kg grouper, Epinephelus sp., was caught at the southwest corner of Johnston Island near the garbage chute. The stomach was full of spiny lobsters (R. E. Brock, pers. commun., February 1984).

An unusual relatively minor injury was found on four of the turtles captured. This consisted of an ulcer on the dorsal neck surface over the supraoccipital bone of the skull. The exact cause is unknown, but could involve repeated abrasion against hard substrate, perhaps the roof of a coral recess where the turtles sleep.

Strandings

Information was obtained on strandings of four turtles. Three were described in interviews with resident personnel, and one by correspondence from the U.S. National Museum concerning the specimen mentioned in Amerson and Shelton (1976).

According to Cris Balubar, a large dead turtle "tangled in a Japanese fish net" washed up near East Peninsula several years ago. Also, at an unknown date a small turtle was found dead on the beach at Akau Island. No other information was available about these two incidents.

Phil Roseberry related that a few years ago he was told by Army personnel about a large dead turtle which washed in at Akau Island. He visited the site the next day, but the turtle was gone, presumably washed away by the next high tide.

Dr. Jack G. Frazier provided the following data on file for the specimen at the U.S. National Museum:

USNM 163581 (Catalogue entry)
 Accession No. - 278016
 Original No. - 11287
 Name - Chelonia mydas/japonica
 Locality - Sand Island, Johnston Atoll
 Date collected - November 20, 1966
 Received from - Smithsonian Institution Pacific Ocean
 Biological Survey Project
 Collected by - --
 When entered - September 14, 1967
 Sex and No. of specimens - 1 head

Dr. Frazier also related that the head is approximately 10 cm wide and preserved in alcohol. It appears to have been collected fresh, and has a cut on the left side similar to what would result from a blow with a machete. This is the extent of information available. A 10-cm wide head would have come from a turtle about 75 cm SCL, hence of an immature size. Cris Balubar was unaware of this specimen, as were the other longtime residents interviewed. A probable scenario might be that a freshly dead turtle washed up at Sand Island from the adjacent ship channel. A short time later it was found by Smithsonian personnel, who used a machete or ax to sever the head for the museum's collection. One of these cuts may have accidentally hit the side of the head. Other possible explanations might be that the gash resulted from a shark attack, or collision with a boat propeller. It seems unlikely that a live healthy turtle of this size would have been collected just for the head, unless the turtle was taken mainly for food or a trophy shell. By itself, and especially with no accompanying data, the head is of little taxonomic value, except to show the presence of Chelonia.

The U.S. National Museum's subspecies designation of japonica is the name sometimes applied to western Pacific green turtles. The type locality is Japan (Hirth 1971). Based on existing information, the use of this or any other trinomial for the Johnston population is not currently justified.

Basking

No evidence was found during the field study that green turtles bask ashore during the daytime, as they commonly do at Johnston's closest island neighbor, French Frigate Shoals in the Northwestern Hawaiian Islands (Whit-tow and Balazs 1982). Balazs (1978) indicated that the turtle collected at Sand Island in 1966 may have been basking (or nesting). However, this now seems unlikely in view of the information presented in the previous section.

Nitta (1982) stated that he received a report of turtles sometimes hauled out during the early morning on the coral-rubble and sand beach between the iron pilings and West Peninsula (Fig. 1). No turtles were found by Nitta (1982) when this site was visited at 0600 on July 9, 1982. Observers in the present study also surveyed the beach, which was 200 m long and accreted against the cement seawall that borders most of Johnston

Island. There were no marks in the beach suggestive of use by turtles. The site was visited on November 15 (2200), 16 (0500, and 2300) and 17 (0500), but no turtles were seen. Cris Balubar reported that the beach is unstable in that portions often wash away and return. He sometimes visits here early in the morning to look for baitfish, but has never seen a turtle ashore. Nevertheless, it is conceivable that turtles do occasionally come out at night to sleep along this shoreline when underwater sleeping sites become unacceptable due to storm surge or other factors. Such behavior is known at Necker Island and Pearl and Hermes Reef (Northwestern Hawaiian Islands), and on the Na Pali coast of Kauai, Hawaii.

An historic absence of basking by turtles at Johnston Atoll may have prompted the comment in 1859 by Brooke (MS.), quoted by Amerson and Shelton (1976), that "The reefs are covered with fish of various kinds. Mullet abound, but there are no turtles." Just 3 months earlier, in January 1859, Captain Brooke had visited French Frigate Shoals and Laysan Island, where he saw many turtles basking on the beach (Amerson 1971; Ely and Clapp 1973). These sights might easily have caused him to believe that land basking was common behavior for all sea turtles at remote Pacific islands. Seeing none along the shoreline at Johnston during his 2-day visit would naturally have come as a surprise, hence causing him to comment about no turtles being there. Since turtles were caught at Johnston 33 years later in 1892 by Captain Cameron (Farrell 1928), Brooke's (MS.) statement could not have been applicable to turtles in the water. It most likely meant that he expected to see turtles on the beach, and that no special search was made for them in the waters of the atoll. It should also be noted that when Captain Brooke arrived, 14 men were already living on Johnston Island, some since July 1858, building a wharf and railway for shipping guano (Amerson and Shelton 1976). Captain Cameron noted the abandoned remains of this facility in 1892 (Farrell 1928).

Reproduction

No historic records are known of turtles nesting at Johnston Atoll, although Amerson and Shelton (1976) speculate that perhaps they did in small numbers before habitation by man. Johnston Island was inhabited intermittently for guano removal starting in July 1858. Sand Island, however, seems to have remained uninhabited until the mid-1930's, when military construction began there.

The nesting season for green turtles in northern latitudes is from May through August. At French Frigate Shoals (lat. 23°45'N), the major nesting site for Hawaiian green turtles, the peak months are June and July. A similar season should exist at Johnston (lat. 16°45'N), if turtles nested there. The Tanager Expedition spent 10 days in July 1923 camped on uninhabited Johnston Island. According to Amerson and Shelton (1976), Wetmore (MS. a and b) "...recorded no turtles." However, from this statement it is unclear if Alexander Wetmore, leader of the expedition, actually noted an absence of turtles, or just made no mention of them in his field journal. The latter case applies for Wetmore (MS. b), but I have not seen Wetmore (MS. a). Nevertheless, while camped on Johnston Island, Wetmore (MS. B) tells of a nighttime walk along the beaches of "fine white coral sand." If

turtles were seen coming ashore to nest in numbers, surely it would have been mentioned. This should also have been the case for any extensive nesting excavations seen in the vegetation zone during numerous daytime surveys. However, it is conjecture if the same would also apply for Sand Island. There were no overnight camps there, and only two daytime visits were made.

It should be noted that the Tanager Expedition had just come from French Frigate Shoals and other Northwestern Hawaiian Islands, where journal notes were in fact made about turtles basking, nesting, and being recently exploited (Amerson 1971). The expedition constituted the first discovery by scientific personnel of sea turtles actually basking. Consequently, most of the interest relating to turtles was focused on this behavioral aspect (Mellen 1925; Wetmore 1925).

The question of whether or not turtles nested at Sand or Johnston Island when the Tanager Expedition visited in 1923 can probably be answered conclusively from aerial photographs. A small seaplane made the first photographic flights over the atoll during the expedition on July 12 and 19 (Wetmore MS. b). These and other U.S. Navy aerial photos taken until the late 1930's should be of sufficient resolution to show nesting excavations, if such sites existed. The original photos are apparently on file in the U.S. National Archives (Amerson and Shelton 1976).

During his residency at Johnston Island since 1962, Cris Balubar only knows of one instance of a possible nesting, but couldn't recall the year. Turtle tracks and digging were seen at Sand Island, but there was no confirmation that eggs were laid. Cris Balubar also stated that he had never seen eggs inside turtles he had caught and cleaned. Upon further discussion, it was determined that only ova of a large and nearly mature size would have been noticed and remembered by him.

Several people interviewed, including Cris Balubar, said that they had seen turtles locked together copulating, sometimes for extended periods. Cris Balubar felt that this mating activity was more prevalent during September through November. Francisco Aguinaldo and Ed Mattson saw a copulating pair in July 1983 at the shoreline of the sand beach by the iron pilings. The turtles swam off quickly when approached. Previous occurrences of this sort may have been partly responsible for the report received by Nitta (1982) of turtles hauling out on this beach. Present accounts of turtles copulating at Johnston are supported by the fact that, in 1892, Captain Cameron tethered a few receptive females to attract and catch males intent on mating (Farrell 1928). The contradiction here is that, for the most part, green turtles are thought to mate only in waters adjacent to their nesting beach.

The lesions typically present on males and females following copulation were not seen on any of the turtles captured in this present study.

A survey of Sand Island's shoreline identified four sand beaches, all located at the eastern end which comprised the original portion of the island before enlargement. Each of these natural beaches offers access to the elevated interior where the soil is suitable for nesting. With the

exception of one beach where there is a bright electrical light, Sand Island presently seems to be appropriate habitat for nesting, if turtles wanted to nest there. Even the beach by the iron pilings on Johnston Island has an elevated area of fine sand where nesting might successfully take place. In contrast, the man-made islands of Akau and Hikina are unsuitable, since the shorelines consist only of cement seawalls and coarse coral rubble, and the interiors are compacted aggregate from dredging.

Migrations

Since there presently is no nesting at Johnston Atoll, and possibly never was, the turtles must be periodically migrating elsewhere to reproduce. This would be consistent with the pattern found in most other green turtle populations, where round trip migrations take place between resident foraging areas and distant breeding grounds. Migrations of this nature are known to be made, even when what may appear to be acceptable nesting beaches are close by. Though not conclusively proven, the turtles are most likely returning to breed at their natal beaches.

A logical place where Johnston's turtles might go to nest would be French Frigate Shoals. This site is only 830 km to the north, and comprises the major rookery for green turtles migrating from islands throughout a 2,200 km expanse of the Hawaiian Archipelago. However, there are no tag recoveries to support the hypothesis of French Frigate Shoals actually being the breeding site for Johnston's turtles. Ample opportunities have existed for such a migratory pattern to be demonstrated. Over the past 20 years, more than 1,600 adults have been tagged at French Frigate Shoals, and about 200 others tagged elsewhere in the Northwestern Hawaiian Islands. None of these tagged turtles has been recovered in the Johnston population, neither in the present study, nor when turtle fishing was allowed at the atoll. Cris Balubar estimates he caught 60 turtles between 1967 and 1976, but found no tags. These same years were some of the most intensive for tagging turtles at French Frigate Shoals. Interestingly, during the years 1966-72, 860 Hawaiian monk seals, Monachus schauinslandi, were also tagged in the Northwestern Hawaiian Islands. Three of these have subsequently been reported at Johnston; one came from French Frigate Shoals, and two from Laysan Island (Schreiber and Kridler 1969; Johnson and Kridler 1983). Monk seals were apparently a conspicuous component of Johnston's fauna when Captain Cameron visited there in 1892 (Farrell 1928). In this century, however, very few seals are known to have migrated outside the Hawaiian Archipelago, and then only to Johnston Atoll. A migratory link between Johnston and French Frigate Shoals also exists for seabirds. Of 733 inter-island tag recoveries, 32% involved French Frigate Shoals (Amerson and Shelton 1976).

The isolated location of Johnston limits the number of other sites the resident turtles might go to nest. The Line Islands, starting with Kingman Reef 1,575 km to the southwest, is the next closest area to Johnston after French Frigate Shoals and the other Northwestern Hawaiian Islands. A low level of green turtle nesting occurs at the inhabited atolls of Fanning and Christmas in this island group. But none is known to occur at Kingman, nor the nearby atoll of Palmyra.

The closest island to the west of Johnston is uninhabited Bikar in the northern Marshall Islands. Bikar is located 2,220 km away and is considered a prominent nesting site for green turtles (Pritchard 1982). No tagging has been conducted at Bikar, so the resident foraging grounds for turtles nesting there are unknown. Presumably they include many of the Marshall Islands. Bikar is a traditional wildlife reserve owned by chiefs of a Marshallese clan who periodically visit to gather turtles, seabirds, and their eggs (Tobin 1952).

Canton and other islands of the Phoenix group are situated almost directly south of Johnston, below the Equator, at a closest distance of 2,160 km. Green turtles have been found to nest here, but again the areas where they migrate from are currently unknown (Balazs 1975).

The limited amount of tagging done in the Pacific has uncovered some impressive long distance migrations by turtles, each encompassing the boundaries of several island nations (Balazs 1982c). Turtles tagged at Johnston in the present study may very well yield similar results, and eventually pinpoint the nesting site.

From interviews, it was learned that three turtles had been marked at Johnston before the tagging done in this study. In 1971, Cris Balubar tagged a turtle (on the dorsal surface of a front flipper) with an aluminum plate embossed with his name, location (Johnston), weight of the turtle (130 lb (59.1 kg)), and date of release. The day and month could not be recalled. He also caught another turtle sometime in 1971 described as being "large and ugly," but apparently not diseased or injured. The carapace of this one was painted completely black before it was released. A second turtle was also marked with paint. This one weighed only about 14 kg and was hand captured by someone else close to shore at Hikina Island. The words "Happy New Year January 1981" were stenciled on the carapace with fluorescent paint. No recoveries have been reported for these three turtles.

Utilization

It is not possible to quantify the number of turtles taken at Johnston over the years, except for the estimate of 60 given by Cris Balubar for 1967-76. An estimate of 12-15 turtles harvested per year by "a long time resident" appears in Amerson and Shelton (1976).

All turtles caught at the atoll since military occupation in the 1930's can be assumed to have been taken for sport, trophy shells, and as a seafood delicacy along with fish and lobster. There is no evidence of commercial harvest during this period, although some shells were probably sold privately. In 1976 the refuge manager for the U.S. Fish and Wildlife Service (Palmer Sekora) prohibited all taking of turtles at Johnston. This measure was instituted to achieve consistency with the already protected status of sea turtles at other National Wildlife Refuges in the United States.

Cris Balubar's case history of turtle fishing is worth describing, since he is well known locally for this skill. He appears to be the only

person over the past 22 years who regularly targeted turtles with a specific fishing technique. This viewpoint could, however, be biased due to Cris Balubar's long residency, and since he is still there to be interviewed. Other personnel fishing just for turtles may have come and gone over the years, leaving no verbal record of their activities. Turtle catching by others was probably only on an opportunistic basis while diving and spearfishing. For instance, some years ago Lee Gohr caught a 59-kg turtle while recreational diving between Sand and North Islands. Also, since turtle fishing has been illegal since 1976, it is unlikely any information would be volunteered about turtles taken thereafter. A secondhand report, believed to be reliable, was received that occasionally turtles are still taken for food when they are accidentally encountered by divers in the north of the atoll. In these instances, it was reported the divers discard the shell and flippers before returning to Johnston Island.

Cris Balubar's turtle fishing started in 1967 when he was asked to catch a turtle for one of the island's military officers. As it is now, most turtles were found along the south shore. West Peninsula was generally off limits for recreational purposes at that time. However, special permission for fishing was granted in this case. The technique successfully employed involved a fiber glass pole with a spinner reel and treble hook to cast out and snag the turtle while it was feeding. A lengthy period would then often be needed to reel it in. The turtle incurred very little physical injury during capture, since it was usually hooked only in a flipper. This fishing method is a modification of one sometimes used for turtles in Hawaii (Balazs 1980c). Cris Balubar subsequently caught turtles in this manner from a small boat off the south shore, as well as from the seawall. He estimates that 45 of the 60 turtles taken were by boat. According to Balubar, Johnston turtles taste much better than Hawaiian turtles. This difference could be due to the algal food sources utilized. A recent article in Hawaii Fishing News describes his snagging technique used to land a large yellowfin tuna from the seawall at Johnston (Balubar 1982).

The only firm evidence of turtles being exploited at Johnston before military settlement is Captain Cameron's mention of their use in 1892 for shark bait and food (Farrell 1928). Turtles, along with seals, were a preferred bait for shark fishing at that time. It is reasonable to assume that other commercial fishing expeditions stopping there would also have taken turtles, if they could be found. In 1918 an attempt was made to establish a fishing station at Johnston, but dissatisfied workers quickly terminated the plan. During the 1920's, at least two commercial fishing vessels visited the atoll. One was the Lanikai, a vessel known to take turtles from Pearl and Hermes Reef for markets in Honolulu (Thurston 1928; Amerson and Shelton 1976; Balazs 1980c). Brock et al. (1965) imply that at least one fishing boat from Honolulu regularly visited Johnston before World War II.

Guano mining outposts on remote Pacific islands, like the one started at Johnston in 1858, regularly used whatever marine resources were available for fresh food. Turtles were among those items eaten by guano diggers on Laysan Island. Presumably turtles were also eaten at other guano islands where they were present. Turtles were also eaten at the intermittent camps

set up illegally by plume hunters in the Northwestern Hawaiian Islands. The remains of such a camp were found at Johnston in 1923 (Wetmore MS. b).

Environmental Perturbations

A number of man-made perturbations have historically taken place at Johnston that could have adversely affected turtles. Some of these impacts, like blasting to remove coral, almost certainly caused direct mortality. Others have possibly been more subtle, thus making them difficult to detect (Whittle et al. 1977). The highly modified environment at Johnston, and the various uncommon activities periodically conducted there, warrant the consideration of these perturbations. It is beyond the scope of this paper to give an in-depth evaluation and analyses of these factors. However, the information contained herein should provide some direction for possible future research of turtles at Johnston Atoll.

Initial blasting and dredging to clear coral and increase the size of Johnston and Sand Islands happened from 1939 to 1942. Woodbury (1946) describes the difficulties experienced in breaking up the coral, and the extraordinary amount of dynamiting required. Johnston Island was expanded from its original 19 ha to 85 ha, and 4-ha Sand Island was doubled in size. Major construction projects to further enlarge Johnston Island were completed in 1958 and 1964, resulting in the present land area of 253 ha. The man-made islands of Akau (10 ha) and Hikina (7 ha), with channels leading to them, were also finished in 1964 (U.S. Army Corps of Engineers 1983). The concussions from underwater explosions during these various projects would have stunned any turtle in the vicinity causing injury and death from direct impact or drowning. Such blasting, and the resulting dead fish, would also be an attractant to large sharks that could, in turn, easily have preyed on stunned turtles. The likelihood that this actually happened is supported by Benson's (1953) description of "...numerous huge sharks" being present during dynamiting, and one of them seen "...swallowing a sea turtle whole." Underwater explosions have also been set off occasionally in recent years. Moses Caballero mentioned the destruction of a live bomb found in the turning basin of the ship channel. It should be noted that some blasting also occurred in the lagoon waters of Johnston long before military activities. During Captain Cameron's 1892 visit, at least one marine harvest was made by driving fish close to shore and setting off "dynamite cartridges" (Farrell 1928: p. 406).

Several hydrogen bombs were successfully detonated at high altitude over Johnston in 1958 and 1962. Amerson and Shelton (1976) stated the following with respect to one of the environmental impacts:

"During these nuclear tests, an elaborate water sprinkler system was installed on the original portion of Sand Island to protect the birds living there. In addition, other protective devices were used, including smoke pots placed upwind as a shade screen and aerial flares to divert the birds' attention from the flash of the blast itself."

Since the flash (and heat?) from these explosions was so intense at ground level, eye damage could presumably have resulted to any turtles on or near the surface at the time of detonation.

During 1962, three of the missiles carrying nuclear devices malfunctioned, exploded, and spread particles of radioactive material over the atoll and surrounding Pacific Ocean. One of these blasts was on the launch pad, significantly affecting a portion of Johnston Island (Anonymous 1962a, 1962b, 1962c). Decontamination efforts have been periodically carried out, including removal and dumping of debris and surface soil over deep water outside the atoll. As a result, some contaminated soil entered the nearshore waters of the island and certain areas of the island continue to be "off limits." The surface runoff of rainfall undoubtedly transports additional particles into the nearshore waters. The soil at the western end of Sand Island is also still contaminated (U.S. Army Corps of Engineers 1983). Benthic algae, including types which exist in the turtle foraging habitat along the south shore, concentrate certain radionuclides at rates higher than other plants and animals (Hines 1962: p. 145-151; Whittle et al. 1977). Hillestad et al. (1974) reported very low levels of gamma emitters in tissue from loggerhead turtles, Caretta caretta, in Georgia and South Carolina. The levels present in turtles from a contaminated area are apparently unknown.

During the early 1970's, various chemical weapons and herbicides were stored on Johnston Island. Also, canisters of dioxin were flown to the atoll in 1976 (Benson 1976). The herbicide was safely incinerated at sea in 1977 using a ship built for such purposes (Nelson 1977). However, leakage from these drums resulted in Herbicide Orange and dioxin contamination of soil at the northwest corner of the island. In 1973, various water, sediment, and marine biological samples were tested for dioxin and Herbicide Orange. A muscle and liver specimen from a green turtle of unknown size, taken between East and West Peninsulas, were included. A sample of Bryopsis, but not Caulerpa, from the same area was also analyzed. None of these four samples from 1973 (presumably measured on a dry matter basis) was found to have detectable levels of dioxin or Herbicide Orange (U.S. Army Corps of Engineers 1983: footnote in Table III-6, Appendix L).

Some leakage of nerve gas from deteriorating munitions containers has been reported (Borg 1982). As noted in a previous section, wash water from the decontamination procedure is discharged through the sewer outfall directly into the turtle foraging habitat. Storm drains may also receive some of this effluent.

A considerable amount of man-made debris was seen on the ocean bottom during diving surveys at locations G and U (Fig. 2). These were the only two offshore (>14 m) sites surveyed; so discarded items may exist over a much broader area off Johnston Island's south shore. The material seen consisted of 55-gal drums, a trailer, a Mike boat, and pieces of iron reinforcement bar. The drums were heavily rusted, but some appeared intact. The contents, if any, could not be determined through interviews with resident personnel.

Heavy metals are known to be discharged from desalination plants as the result of internal corrosion. Two types of discharge have been reported: one emitted when the plant is operating normally, the other produced during periodic cleaning and maintenance cycles (Chesher 1975).

High levels of copper are present in the normal effluent, and this element is believed to be the most toxic to marine organisms. When desalination plants shut down for maintenance, corroded copper-nickel surfaces dry and oxidize. With resumption of operation, copper contamination is 2-3 times higher than normal for a few hours. Higher levels of nickel and iron are also released. The discharge during this period is turbid and black (Chesher 1975). Few studies have attempted to measure heavy metal content in sea turtles and their eggs (Hillestad et al. 1974; Stoneburner et al. 1980; Witkowski and Frazier 1982). Furthermore, as emphasized by Witkowski and Frazier (1982) and Coston-Clements and Hoss (1983), it is difficult to determine the significance of such findings because little is known about baseline levels and physiological effects. Based on reports of copper levels discharged from a desalination plant (Chesher 1975), the facility at Johnston probably produces at present 1.3-2.6 kg of copper effluent per day under normal operation. Effluent from the plant apparently also serves to enrich, by some undetermined process, the existing radionuclide contamination in nearshore waters, thereby producing a localized "hot spot" (U.S. Army Corps of Engineers 1983: Appendix L, p. 5-6). Whether or not cooling water from other facilities besides desalination would do the same is unknown.

Petroleum spills can adversely affect turtles by external fouling, ingestion, and interference with olfactory perception and food supply (Coston-Clements and Hoss 1983). During the field study at Johnston, dried petroleum matter was found adhering to the seawall at the east corner of West Peninsula. It had likely gathered and washed up there from the funneling effect of prevailing winds and currents. The age of the material, and the length of time required for it to accumulate, could not be determined. Turtle foraging habitat around West Peninsula, and along much of the south shore, appears to be vulnerable to petroleum contamination due to its windage and proximity to the ship channel.

Artificial illumination on beaches is known to discourage adult turtles from nesting and disorient hatchlings crawling to the sea (Coston-Clements and Hoss 1983). However, almost no information exists on the effects of coastal lights on turtles foraging or sleeping at night in nearshore habitat. Nocturnal feeding is common behavior for green turtles in Hawaii (Balazs 1980c). However, at Johnston the catch rates from nets, and direct observations made from shore, suggest that foraging is mostly, if not entirely, during the daytime. Between West Peninsula and the island's southwest corner there are nine white lights of medium intensity set on posts 75-100 m inland. In addition, 23 dim yellow lights are located on the chemical storage bunkers facing the shoreline. None of these lights directly illuminate the nearshore waters, although they are clearly visible from offshore. At present, there are no lights on posts anywhere near the shoreline of West Peninsula itself.

Cholinesterase

Very low concentrations of organophosphorus compounds inhibit the activity of cholinesterase, an enzyme responsible for important physiological processes in the nervous system. Cholinesterase also occurs in serum and red blood cells. The inhibitory effect of organophosphorus

compounds is the basis for their use as insecticides and certain chemical weapons. Cholinesterase inhibition can also be used to biochemically detect organophosphorus compounds in the environment or in an organism (Namba 1971; Lundin 1975).

At Johnston Island, red blood cell cholinesterase is measured in humans by the 17-Minute Manual Method. According to information supplied by Lucille Bodnar, who routinely performs this analysis at Johnston, the method is based on the principle that cholinesterase hydrolyzes acetylcholine bromide with the production of acetic acid. The change in pH is measured in a barbital-phosphate buffer when red blood cells are mixed with a known excess of acetylcholine bromide and allowed to hemolyze. The results are expressed in terms of the decrease in pH units during the 17-minute reaction period. The normal range for humans is 0.63-0.89 pH/h.

Cholinesterase values, using a 0.2 ml aliquot of red blood cells, were determined by this method for six adult and three immature turtles (Table 13). The validity of these results is unknown, since the analysis is designed for human blood. The method may be unsuitable for turtle blood due to the capacity of the buffer, size of aliquot used, or other factors. Verification is needed. In addition, the normal range of decrease in pH units for the green turtle is currently unknown. Given these analytical uncertainties and the small numbers sampled, Table 13 shows that cholinesterase for the nine turtles ranged from 0.13 to 0.34 pH/h. It is worth noting that the mean value for the three adult males (0.27 pH/h) was almost double the mean of the three adult females (0.14 pH/h). Also, the two immature females measured had levels similar to the adult males. Two of the nine turtles sampled were caught at net location 7, downwind of the sewer outfall. There is no indication from these few data that differences exist between sampling locations.

RECOMMENDATIONS

Management Measures

The information contained in this paper provides a basis for offering recommendations of management measures to help ensure the conservation of turtles at Johnston Atoll. These actions are:

1. A specific management zone for marine turtles should be established. The area should encompass marine habitat extending seaward for about 1 km along the entire south shore of Johnston Island, as well as a contiguous band extending about 1.5 km to the northeast of the main ship channel. The purpose of this zone would be to give special attention to the turtles concentrated there and the habitat upon which they depend. An appropriate and distinct mechanism would then exist to soundly manage the area on a continuing basis. The designation would be particularly helpful for identifying and evaluating any potential impacts to turtles and habitat that might arise in the future. The zone would be fully consistent with the environmental goals of the JACADS project and, in fact, the project would likely benefit from the special management attention given to the turtles.

2. A management action needed at present is the curtailment of any recreational boats transiting or anchoring in the area described above. The rapid diving response when turtles are approached by boats indicates that normal foraging behavior is easily disrupted. This may be the result of previous human harassment, including fishing efforts to hook them and regular encounters with small boats.
3. A formal system should be implemented to deal with any future strandings of dead or live turtles. Rapid reporting, and the appropriate immediate response by interested parties, is absolutely essential for these cases. Valuable specimens and data can be acquired in this manner; for example, bones for age determination, whole stomach contents, tissue samples, and a determination of the cause of death or debilitation. The presence of a tag further increases the worth of the specimen. The system should also include turtles or their parts found in the stomach of sharks and other predators.
4. An informative, interesting, and inexpensive brochure, preferably with illustrative photographs, should be prepared telling about the turtles at Johnston, where they principally occur, and their protected status under the U.S. Endangered Species Act. The brochure should be specific for turtles, and not done in descriptive combination with other wildlife or marine resources of the atoll. The brochure should be distributed at the air terminal to each new person upon arrival.
5. A formal response plan should be prepared describing the actions to be taken in the event of a petroleum spill involving the area described for a turtle management zone. Special attention should be given to sites around West Peninsula where spillage may concentrate.
6. A plan to assess the effects, if any, of newly installed lights on the foraging behavior and other use patterns of green turtles off West Peninsula should be developed. This should encompass the temporary lights needed during active construction of JACADS, as well as permanent security lights planned for the completed facility.

Future Research Activities

The successful long-term management of these turtles is, to a large extent, dependent upon a certain amount of future research being accomplished. Research on turtles at Johnston has long been neglected. However, from this present assessment it is apparent that they constitute an ecologically important, scientifically challenging, and historically interesting part of the atoll's fauna. In addition, Johnston's turtles are most likely used for food by native people somewhere in the Pacific islands, since it is doubtful they nest at French Frigate Shoals where full protection would be afforded. A major research and management goal

should be to determine the international migrations of these turtles, including their ultimate destination and island areas of transit where fishing may occur. The only way to achieve this objective at an early date is to capture and tag more turtles at Johnston. The relatively high proportion of adults and females found in the population will be an advantage to understanding the movement patterns, since it will increase the probability of long-distance recoveries.

The following recommendations relate to research that should be accomplished to facilitate a better understanding of the biology of this turtle population. The information developed in these studies will also serve as a basis to formulate future management measures for Johnston's turtles. While this research is clearly needed, it is outside the scope of this paper to indicate specific agency responsibility or priorities for support of this work.

1. A standard monitoring program should be established to assess and tag turtles periodically in a manner similar to the present study. This action will be particularly important during the active construction phase of the JACADS project. During this period, three 10-day study visits per year are deemed necessary. Thereafter, one or two visits per year would be sufficient.
2. Diving surveys with scuba should be made between West Peninsula and the southwest corner of Johnston Island to search for turtle sleeping areas. To accomplish the dives safely, formal arrangements must be made to delay, for 2 h daily, the interval pumping of sewage from the outfall over a 3-4 day period. This appears feasible at present during midmorning when water usage is normally low. However, it must be done before the large increase in personnel scheduled for the JACADS project.
3. The blood analysis used in the present study to measure cholinesterase should be evaluated and, if needed, modified to obtain accurate measurements. Routine testing of cholinesterase in turtles should be conducted as part of the periodic monitoring suggested in recommendation 1 above. The normal range for green turtles should be determined from blood sampling currently underway in Hawaii.
4. The enrichment of radionuclide contamination by effluent from the desalination plant should be elucidated. The possible role of heat and heavy metals in this process should be examined to ascertain if discharge water planned for JACADS will produce similar enrichment, which in turn may be transferred to turtles through algal food sources.
5. Aerial photographs taken over Johnston Atoll should be located and examined to determine the past distribution of benthic algae and if nesting occurred during the period before large scale inhabitation by man.

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LITERATURE CITED

- Amerson, A. B., Jr. 1971. The natural history of French Frigate Shoals, Northwestern Hawaiian Islands. Atoll Res. Bull. 150:1-383.
- Amerson, A. B., Jr., and P. C. Shelton. 1976. The natural history of Johnston Atoll, central Pacific Ocean. Atoll Res. Bull. 192:1-479.
- Anonymous. 1962a. Warhead detonation is averted. The Honolulu Advertiser, July 27, 1962.
- 1962b. Site repairs may take up to eight weeks. Honolulu Star-Bulletin, July 31, 1962, p. 1.

- Anonymous. 1962c. Destroys Johnston N-shot. The Honolulu Advertiser, Oct. 16, 1962, p. 1-2.
- Applied Eco-Tech Services, Inc. 1983. Johnston Atoll water quality and current study - a final report. Report submitted to U.S. Army Engineer District, Honolulu, 24 Aug. 1983, 100 p.
- Balazs, G. H. 1975. Marine turtles in the Phoenix Islands. Atoll Res. Bull. 184:1-7.
1976. Green turtle migrations in the Hawaiian Archipelago. Biol. Conserv. 9:125-140.
1978. Terrestrial critical habitat for sea turtles under United States jurisdiction in the Pacific region. 'Elepaio 39(4):37-41.
- 1980a. Field methods for sampling the dietary components of green turtles, Chelonia mydas. Herpetol. Rev. 11(1):5-6.
- 1980b. A review of basic biological data on the green turtle in the Northwestern Hawaiian Islands. In R. W. Grigg and R. T. Pfund (editors), Proceedings of the Symposium on Status of Resource Investigations in the Northwestern Hawaiian Islands, April 24-25, 1980, University of Hawaii, Honolulu, Hawaii, p. 42-54. Sea Grant Misc. Rep. UNIHI-SEAGRANT-MR-80-4.
- 1980c. Synopsis of biological data on the green turtle in the Hawaiian Islands. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-7, 141 p.
- 1982a. Factors affecting the retention of metal tags on sea turtles. Mar. Turtle News1. 20:11-14.
- 1982b. Growth rates of immature green turtles in the Hawaiian Archipelago. In K. A. Bjorndal (editor), Biology and conservation of sea turtles, p. 117-125. Smithsonian. Inst. Press, Wash., D.C.
- 1982c. Sea turtles: A shared resource of the Pacific islands. South Pac. Comm. Fish. News1. 23:22-24.
- 1982d. Status of sea turtles in the central Pacific Ocean. In K. A. Bjorndal (editor), Biology and conservation of sea turtles, p. 243-252. Smithsonian. Inst. Press, Wash., D.C.
1983. Recovery records of adult green turtles observed or originally tagged at French Frigate Shoals, Northwestern Hawaiian Islands. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-36, 42 p.
- Balubar, C. 1982. Biggest fish story--mail buoy. Hawaii Fish. News 7(10):8.

- Benson, B. 1953. Johnston Island--it's not exactly paradise. Honolulu Star-Bulletin, Nov. 8, 1953, magazine section, p. 15.
1976. Air Force flies deadly dioxin canisters to Johnston Atoll. The Honolulu Advertiser, Dec. 9, 1976, A:14.
- Bentley, T. B., and A. Dunbar-Cooper. 1980. A blood sampling technique for sea turtles. Final report for contract No. NA-80-GE-A-00082, Southeast Fisheries Center, National Marine Fisheries Service, NOAA, 14 p.
- Borg, J. 1982. Nerve gas leaks seen under control. The Honolulu Advertiser, Nov. 4, 1982, A:5.
- Brock, R. E. 1972. A contribution to the biology of Gymnothorax javanicus (Bleeker). M.S. Thesis, Univ. Hawaii, 121 p.
- Brock, V. E., R. S. Jones, and P. Helfrich. 1965. An ecological reconnaissance of Johnston Island and the effects of dredging. Univ. Hawaii, Hawaii Mar. Lab., Tech. Rep. 5, 90 p.
- Brock, V. E., W. Van Henkelem, and P. Helfrich. 1966. An ecological reconnaissance of Johnston Island and the effects of dredging. Second Annual Report. Univ. Hawaii, Hawaii Mar. Lab., Tech. Rep. 11, 56 p.
- Brooke, J. M. MS. Journal of the Fenimore Cooper for 1859. [Unpublished manuscr.] G. M. Brooke, Jr., Lexington, Va.
- Buggeln, R. G., and R. T. Tsuda. 1966. A preliminary marine algal flora from selected habitats on Johnston Atoll. Univ. Hawaii, Hawaii Inst. Mar. Biol., Tech. Rep. 9, 29 p.
1969. A record of benthic marine algae from Johnston Atoll. Atoll Res. Bull. 120:1-20.
- Carr, A. 1972. Great reptiles, great enigmas. Audubon 74(2):24-35.
- Chesher, R. H. 1975. Biological impact of a large-scale desalination plant at Key West, Florida. In E. J. Ferguson Wood and R. E. Johannes (editors), Tropical marine pollution, p. 99-153. Elsevier Oceanogr. Ser. 12.
- Coston-Clements, L., and D. E. Hoss. 1983. Synopsis of data on the impact of habitat alteration on sea turtles around the southeastern United States. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-SEFPC-117, 57 p.
- Dawes, C. J., and R. H. Goddard. 1978. Chemical composition of the wound plug and entire plants for species of the coenocytic green alga, Caulerpa. J. Exp. Mar. Biol. Ecol. 35:259-263.
- Ely, C. A., and R. B. Clapp. 1973. The natural history of Laysan Island, Northwestern Hawaiian Islands. Atoll Res. Bull. 171:1-361.

- Farrell, A. (transcriber). 1928. John Cameron's odyssey. The MacMillan Co., 461 p.
- Glazebrook, J. S., R. S. F. Campbell, and D. Blair. 1981. Pathological changes associated with cardiovascular trematodes (Digenea: Spirorchidae) in a green sea turtle Chelonia mydas (L). J. Comp. Pathol. 91:361-368.
- Harshbarger, J. C. 1977. Role of the registry of tumors in lower animals in the study of environmental carcinogenesis in aquatic animals. In H. F. Kraybill, C. J. Dawe, J. C. Harshbarger, and R. J. Tardiff (editors), Aquatic pollutants and biologic effects with emphasis on neoplasia, p. 280-289. New York Acad. Sci., N.Y.
- Hillestad, H. O., R. J. Reimold, R. R. Stickney, H. L. Windom, and J. H. Jenkins. 1974. Pesticides, heavy metals and radionuclide uptake in loggerhead sea turtles from South Carolina and Georgia. Herpetol. Rev. 5(3):75.
- Hines, N. O. 1962. Proving ground. Univ. Washington Press, Seattle, 366 p.
- Hirth, H. F. 1971. Synopsis of biological data on the green turtle Chelonia mydas (Linnaeus) 1758). FAO Fish. Synop. 85, 1:1-8:19.
- Ireland, L. C. 1979a. Homing behavior of immature green turtles (Chelonia mydas). Am. Zool. 19:952.
- 1979b. Homing behavior of juvenile green turtles, Chelonia mydas. In C. J. Amlaner, Jr., and D. W. MacDonald (editors), A handbook of biotelemetry and radio tracking, p. 761-764. Pergamon Press, Oxford.
- Jacobson, E. R. 1981. Virus associated neoplasms of reptiles. In C. J. Dawe, J. C. Harshbarger, S. Kondo, T. Sugimura, and S. Takayama (editors), Phyletic approaches to cancer, p. 53-58. Jpn. Sci. Soc. Press, Tokyo.
- Johnson, A. M., and E. Kridler. 1983. Interisland movement of Hawaiian monk seals. 'Elepaio 44(5):43-46.
- Ludwig, G. M. 1982. Trip report: Johnston Atoll, September 12-17, 1981. U.S. Fish and Wildlife Service, Honolulu, 20 p.
- Ludwig, G. M., S. Fefer, J. Maragos, and E. Nitta. 1982. JACADS project environmental survey at Johnston Atoll NWR July 8-11, 1982. Trip report. U.S. Fish Wildl. Serv., Honolulu, 21 p.
- Lundin, S. J. 1975. The inhibition of cholinesterase activity by organophosphorus compounds as a means of an inspection procedure. In The problem of chemical and biological warfare. Vol. VI. Technical aspects of early warning and verification, p. 177-183. Humanities Press, N.Y.

- Meinesz, A. J. Jaubert, and M. Denizot. 1981. Distribution of the algae belonging to the genus Caulerpa in French Polynesia (atoll of Takapoto and island of Moorea). Proceedings of the Fourth International Coral Reef Symposium, Manila 2:431-437.
- Mellen, I. M. 1925. Marine turtles sleep on Hawaiian sands. N.Y. Zool. Soc., Bull. 28:160-161.
- Menzies, R. A., L. Kochinsky, J. M. Kerrigan. 1983. Techniques for muscle biopsy and blood sampling from sea turtles. Poster session presented at the Western Atlantic Turtle Symposium, July 17-22, 1983, San Jose, Costa Rica, 2 p.
- Namba, T. 1971. Cholinesterase inhibition by organophosphorus compounds and its clinical effects. Bull. WHO 44:289-307.
- Nelson, L. 1977. Herbicide burning to end this week. Honolulu Star-Bulletin, July 27, 1977, C:4.
- Nitta, E. T. 1982. Johnston Atoll field trip report, July 1982. Southwest Region, Western Pacific Program Office, Natl. Mar. Fish. Serv., NOAA, Honolulu, 6 p.
- Owens, D. W., and G. J. Ruiz. 1980. New methods of obtaining blood and cerebrospinal fluid (from marine turtles). Herpetologica 36:17-20.
- Paul, V. J. 1983. Strategies of chemical defense in tropical marine algae of the order Caulerpaceae (Chlorophyta). (Abstract.) 64th Annual Meeting of the Western Society of Naturalists, Burnaby, British Columbia.
- Paul, V. J., and W. Fenical. 1982. Toxic feeding deterrents from the tropical marine alga Caulerpa bikiniensis (Chlorophyta). Tetrahedron Lett. 23, 48:5017-5020.
- Pritchard, P. C. H. 1982. Marine turtles of the South Pacific. In K. A. Bjorndal (editor), Biology and conservation of sea turtles, p. 253-262. Smithsonian Inst. Press, Wash., D.C.
- Rainey, W. E. 1981. Guide to sea turtle visceral anatomy. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SEFC-82, 82 p.
- Randall, J. E. 1980. A survey of ciguatera at Enewetak and Bikini, Marshall Islands, with notes on the systematics and food habits of ciguatera toxic fishes. Fish. Bull., U.S. 78:201-249.
- Russell, D. J., and B. A. Carlson. 1978. Edible-oil pollution on Fanning Island. Pac. Sci. 32:1-15.
- Schreiber, R. W., and E. Kridler. 1969. Occurrence of an Hawaiian monk seal (Monachus schauinslandi) on Johnston Atoll, Pacific Ocean. J. Mammal. 50:841-842.

- Stoneburner, D. L., M. N. Nicora, and E. R. Blood. 1980. Heavy metals in loggerhead sea turtle eggs (Caretta caretta). Evidence to support the hypothesis that demes exist in the western Atlantic population. J. Herpetol. 14:171-175.
- Thurston, L. A. 1928. Features of Johnston Island. The Honolulu Advertiser, Aug. 5, 1928, p. 4, 11.
- Tobin, J. E. 1952. Land tenure in the Marshall Islands. Atoll Res. Bull. 11:1-36.
- U.S. Army Corps of Engineers. 1983. Johnston Atoll chemical agent disposal system (JACADS) - Final Environmental Impact Statement, 1 Nov. 1983. Pacific Ocean Division, Corps of Engineers, Ft. Shafter, Hawaii, 75 p. + Appendices A-M.
- U.S. Fish and Wildlife Service. MS. Pacific Islands National Wildlife Refuges: Johnston Atoll NWR, Baker Island NWR, Howland Island NWR, Jarvis Island NWR. U.S. Fish and Wildlife Service, Honolulu, Hawaii.
- Votaw, H. C. 1943. Johnston Island. U.S. Naval Institute Proceedings, 69, 487:1176-1180.
- Wetmore, A. 1925. Bird life among lava rock and coral sand. Natl. Geogr. Mag. 59:76-108.
- MS. a. Field notes, 1923. [Unpublished manuscript.] Smithsonian Inst., Wash. D.C.
- MS. b. A scientific survey of Johnston Island, 1923, 25 p. [Unpublished manuscript. prepared in 1963.] [Page 5 missing from copy seen on file at the U.S. Fish and Wildlife Service, Honolulu.]
- Whittle, K. J., R. Hardy, A. V. Holden, R. Johnson, and R. J. Pentreath. 1977. Occurrence and fate of organic and inorganic contaminants in marine animals. In H. F. Kraybill, C. J. Dawe, J. C. Harshbarger, and R. J. Tardiff (editors), Aquatic pollutants and biologic effects with emphasis on neoplasia, p. 47-79. New York Acad. Sci., N.Y.
- Whittow, G. C., and G. H. Balazs. 1982. Basking behavior of the Hawaiian green turtle (Chelonia mydas). Pac. Sci. 36:129-139.
- Witkowski, S. A., and J. G. Frazier. 1982. Heavy metals in sea turtles. Mar. Pollut. Bull. 13:254-255.
- Woodbury, D. O. 1946. Builders for battle. E. P. Dutton and Co., N.Y., 415 p.

Table 1.--Results of turtle netting effort in meter-hours (MH).

Net location	Phase 1			Phase 2			Total		
	MH	per turtle	Number captured	MH	per turtle	Number captured	MH	per turtle	Number captured
1	4,460	1,115	4	1,975	1,975	1	6,435	1,287	5
2	509		0	4,206	526	8	4,715	589	8
3	1,085	362	3	3,513		0	4,598	1,533	3
4	567		0	---		---	567		0
5	1,026		0	---		---	1,026		0
6	216		0	---		---	216		0
7	---		---	2,748	550	5	2,748	550	5
8	---		---	280		0	280		0
9	---		---	400		0	400		0
10	---		---	340		0	340		0
11	---		---	949		0	949		0
12	---		---	820		0	820		0
13	---		---	153		0	153		0
14	---		---	340		0	340		0
15	---		---	420		0	420		0
16	---		---	420		0	420		0
17	---		---	189		0	189		0
Total	7,863	1,123	7	16,753	1,197	14	24,616	1,172	21

Table 2.--Daily turtle netting effort.

Date 1983	Net location	Number captured	Duration in hours	Length of net (m)	Netting effort (meter-hours)
<u>Phase 1</u>					
10/3-10/7	1	4	94.5	40	3,780
10/4-10/5	2		20	9	180
10/5-10/7	3	2	47	9	423
10/5-10/6	4		21	27	567
10/6-10/7	5		21	27	567
10/7-10/8	1		17	40	680
10/7-10/8	5		17	27	459
10/8-10/11	3	1	73.5	9	662
10/9-10/10	2		23.5	14	329
10/11	6		8	27	216
Subtotal		7			7,863
<u>Phase 2</u>					
11/4	3		10.5	40	420
11/4	2		10	27	270
11/5	2		10.5	40	420
11/5	1		8.5	40	340
11/5	3		6	27	162
11/6	2	2	9.5	27	257
11/6	3		9.5	40	380
11/6	7		7	40	280
11/6	8		7	40	280
11/7	7	1	10	40	400
11/7	9		10	40	400
11/7	2	1	8.5	27	230
11/7	3		8.5	40	340
11/8	2	1	9.5	27	257
11/8	3		9.5	40	380
11/8	7	2	8.5	40	340
11/8	10		8.5	40	340
11/9	3		10.5	40	420
11/9	11		10.5	40	420

Table 2.--Continued.

Date 1983	Net location	Number captured	Duration in hours	Length of net (m)	Netting effort (meter-hours)
11/9	2		9	27	243
11/9	1		9	40	360
11/10	1		9.5	40	380
11/10	2	2	9.5	40	380
11/10	3		8.5	46	391
11/10	11		8.5	40	340
11/11	2		10	40	400
11/11	7	2	10	40	400
11/11	12		10	40	400
11/11	3		10	18	180
11/11	1	1	5	27	135
11/12	2	1	10.5	18	189
11/12	3		10.5	40	420
11/12	7		10.5	40	420
11/12	12		10.5	40	420
11/12	2		8.5	77	230
11/13	1		8.5	40	340
11/13	2	1	8.5	27	230
11/13	7		8.5	40	340
11/13	13		8.5	18	153
11/13	14		8.5	40	340
11/14	1		10.5	40	420
11/14	2		10.5	40	420
11/14	11		10.5	18	189
11/14	7		10.5	27	284
11/14	15		10.5	40	420
11/15	2		10.5	40	420
11/15	3		10.5	40	420
11/15	7		10.5	27	284
11/15	16		10.5	40	420
11/15	17		10.5	18	189
11/16	2		6.5	40	260
Subtotal		14			16,753
Total		21			24,616

Table 3.--Tag numbers, capture sites, and straight carapace lengths of green turtles.

Tag No. ¹	Date 1983	Time of capture	Net location	Straight carapace length (cm)	
				Midline to posterior of postcentral	Midline to of notch
7451-55	10/4	0700	1	100.1	99.8
7485-89	11/6	1500	2	95.9	94.9
7565-69	11/13	1730	2	92.5	92.9
7461-65	10/5	1330	1	90.9	89.6
7490-94	11/7	1600	7	89.7	89.5
7500-04	11/8	1600	2	89.5	88.7
7512-16	11/10	0930	2	89.0	88.8
7468-72	10/6	1730	1	88.2	--
7456-60	10/4	1300	1	87.4	86.9
7560-64	11/12	1600	2	87.0	--
7473-75	10/7	1230	3	84.0	83.6
7521-25	11/11	1500	7	83.7	83.6
7517-20	11/10	1600	2	83.3	83.3
7495-99	11/7	1230	2	82.9	82.1
7555-59	11/11	1700	1	79.1	78.3
7476-80	10/11	1500	3	77.2	76.5
7509-11	11/8	1700	7	75.6	75.2
7505-08	11/8	1700	7	75.2	74.5
7551-54	11/11	1500	7	75.2	74.8
7481-84	11/6	1130	2	72.8	72.1
7466-67	10/5	1830	3	57.4	--

¹Tag series used at Johnston Atoll--7451-7525 and 7551-7569.

Table 4.--Body measurements and weights of green turtles.

Tag No.	Carapace length		Carapace width		Plastron length (cm)	Tail length (cm)	Head width (cm)	Weight (kg)
	Straight (cm)	Curved (cm)	Straight (cm)	Curved (cm)				
7451	100.1	107.8	83.2	105.5	81.1	25.6	13.5	--
7485	95.9	103.7	72.5	94.8	80.2	26.5	12.8	151.4
7565	92.5	96.7	72.1	96.0	79.3	26.4	12.6	141.8
7461	90.9	97.5	69.8	90.6	73.1	20.2	12.1	--
7590	89.7	94.5	71.6	88.5	67.5	¹ 41.7	11.6	115.9
7500	89.5	96.0	68.8	85.5	72.4	25.2	11.9	--
7512	89.0	95.0	67.3	86.5	70.8	¹ 54.6	12.3	114.1
7468	88.2	92.6	71.6	86.0	70.9	¹ 44.0	12.1	--
7456	87.4	95.4	70.4	94.6	72.8	21.0	11.2	--
7560	87.0	92.6	67.4	85.3	70.6	21.2	12.0	108.6
7473	84.0	90.5	65.4	94.5	70.0	21.0	12.0	96.4
7521	83.7	92.2	62.2	80.0	67.2	² --	11.4	85.9
7517	83.3	87.2	64.6	82.0	68.2	³ --	--	84.5
7495	82.9	89.2	65.4	80.6	68.3	18.2	11.3	87.7
7555	79.1	84.5	61.6	79.0	64.0	18.2	10.7	74.1
7476	77.2	84.5	59.6	82.0	61.2	14.5	10.2	67.7
7509	75.6	82.0	57.0	77.8	--	--	10.3	68.2
7505	75.2	81.5	57.8	75.5	60.4	17.0	9.9	65.0
7551	75.2	80.0	61.2	77.6	59.8	14.5	10.9	62.3
7481	72.8	79.1	58.1	76.2	59.3	12.5	9.7	63.6
7466	57.4	63.0	46.3	58.0	44.0	9.5	7.1	--

¹Adult male.²Short deformed tail--no indication of being a male.³Adult male--tail partly amputated.

Table 5.--Front flipper measurements and scale counts of green turtles.

Tag No.	Straight carapace length (cm)	Flipper width ¹		Flipper scales		Postocular scales	
		Left	Right	Left	Right	Left	Right
7451	100.1	14.1	14.4	7	6	3	4
7485	95.9	14.9	15.3	6	6	4	4
7565	92.5	14.0	14.3	6	6	4	4
7461	90.9	13.2	13.4	6	6	4	4
7490	89.7	13.6	13.5	6	6	4	4
7500	89.5	14.7	14.6	6	6	4	4
7512	89.0	15.4	15.0	6	6	4	4
7468	88.2	14.2	14.5	6	6	5	4
7456	87.4	12.4	12.6	5	5	4	4
7560	87.0	13.2	13.2	6	6	4	4
7473	84.0	13.4	13.2	6	6	4	4
7521	83.7	12.6	12.8	6	6	4	4
7517	83.3	14.7	14.6	6	6	4	4
7495	82.9	12.0	12.0	6	6	4	4
7555	79.1	13.1	13.1	6	6	5	4
7476	77.2	11.9	11.0	6	6	4	4
7509	75.6	12.4	12.0	6	6	4	5
7505	75.2	11.0	11.2	6	6	4	4
7551	75.2	12.0	11.2	6	6	4	4
7481	72.8	11.2	10.3	6	6	4	4
7466	57.4	--	--	6	6	4	4

¹Straight line measurement taken from the anterior distal edge of the claw scale to the scale located directly across on the flipper's trailing edge (usually scale No. 6 counting proximal to distal along the trailing edge).

Table 6.--Sex determination of green turtles.

Tag No.	Straight carapace length (cm)	Tail length ¹ (cm)	Testosterone level ²	Sex
7451	100.1	25.6	--	Female
7485	95.9	26.5	<11.1	Female
7565	92.5	26.4	--	Female
7461	90.9	20.2	--	Female
7490	89.7	41.7	11,248.6	Male
7500	89.5	25.2	<11.1	Female
7512	89.0	54.6	561.6	Male
7468	88.2	44.0	--	Male
7456	87.4	21.0	--	Female
7560	87.0	21.1	13.3	Female
7473	84.0	21.0	--	Female
7521	83.7	³ --	13.9	Female
7517	83.3	⁴ --	2,324.9	Male
7495	82.9	18.2	13.7	Female
7555	79.1	18.2	418.7	Male
7476	77.2	14.5	--	--
7509	75.6	--	--	--
7505	75.2	17.0	<11.1	Female
7551	75.2	14.5	--	--
7481	72.8	12.5	26.1	Female
7466	57.4	9.5	<11.1	Female
Total				13 Females 5 males

¹Straight line measurement from the posterior midline edge of the plastron to the tip of the extended tail.

²Testosterone level in the blood in picograms per milliliter (10⁻¹²g/ml).

³Short deformed tail--no indication of being a male.

⁴Adult male--tail partly amputated.

Table 7.--Identification of stomach contents sampled from green turtles.

Tag No.	Straight carapace length (cm)	Sex	Capture site (net location)	Contents
7451	100.1	Female	1	<u>Oscillatoria</u> sp. (trace filaments)
7565	92.5	Female	2	<u>Bryopsis pennata</u> var. <u>secunda</u> <u>Oscillatoria</u> sp. Unidentified amphipod. ¹ <u>Pyxidula</u> sp. (diatoms-trace)
7461	90.9	Female	1	<u>Zonaria</u> sp. (trace-filament)
7512	89.0	Male	2	<u>Caulerpa racemosa</u> var. <u>uvifera</u> <u>Climacosphenia</u> sp. (diatoms-trace) <u>Oscillatoria</u> sp. (trace-filament)
7473	84.0	Female	3	Unidentified fibers-trace
7495	82.9	Female	2	<u>Climacosphenia</u> sp. (diatom-trace) Unidentified filamentous bacteria
7476	77.2	--	3	<u>B. pennata</u> var. <u>secunda</u>
7466	57.4	Female	3	<u>B. pennata</u> var. <u>secunda</u> <u>Polysiphonia</u> sp. (fragment)

¹Probably originated from the esophagus.

Table 8.--Identification of mouth and fecal contents sampled from green turtles.

Tag No.	Straight carapace length (cm)	Sex	Capture site (net location)	Contents
<u>Mouth contents</u>				
7485	95.9	Female	2	<u>Caulerpa racemosa</u> var. <u>macrophyssa</u> <u>Acrochaetium</u> sp. (epiphytic on <u>Caulerpa</u>)
7565	92.5	Female	2	<u>Bryopsis pennata</u> <u>Oscillatoria</u> sp. filaments <u>Pyxidicula</u> sp. (diatoms) Unidentified amphipod
7560	87.0	Female	2	<u>Bryopsis pennata</u> var. <u>secunda</u> <u>Pyxidicula</u> sp. (diatoms)
7555	79.1	Male	1	<u>Caulerpa racemosa</u> var. <u>macrophyssa</u> Unidentified filamentous bacteria Unidentified blue-green algae
7481	72.8	Female	2	<u>Bryopsis pennata</u>
<u>Fecal contents</u>				
7509	75.6	-- ¹	7	<u>Caulerpa racemosa</u> var. <u>uvifera</u> (75%) <u>Bryopsis pennata</u> (25%)

¹Not determined.

Table 9.--Algae collected during diving surveys with scuba.

Dive No.	Date 1983	Location	Algae collected
10	10/10	J	<u>Bryopsis pennata</u> var. <u>secunda</u> (Harvey) Collins and Harvey <u>Caulerpa racemosa</u> var. <u>macrophyssa</u> (Kutzing) Taylor <u>C. racemosa</u> var. <u>uvifera</u> (Turner) Weber von Bosse <u>C. serrulata</u> (Forsk.) J. Ag.
11	10/11	K	<u>C. serrulata</u> f. <u>angusta</u> (Weber von Bosse) Taylor <u>C. serrulata</u> (Forsk.) J. Ag. <u>Dictyota friabilis</u> Setchell (epiphytic on <u>Caulerpa</u>)
13	11/4	M	<u>Celidium pusillum</u> <u>Ceramium</u> sp. (trace)
14	11/5	N	<u>Caulerpa serrulata</u> <u>Avrainvillea lacerata</u> <u>Hydrocoleum lyngbyaceum</u> <u>Zonaria</u> sp. <u>Polysiphonia</u> sp. (trace)

Table 10.--Percent nutrient composition of principal food sources used by green turtles.¹

Algae	Dry matter	Crude protein ³	Ether extract	Ash	Neutral detergent fiber ²	Acid detergent fiber ²	
						Permanganic lignin	Cellulose
<u>Bryopsis pennata</u> var. <u>secunda</u> (from foraging site)	7.0	23.8	2.0	38.2	25.6	2.7	7.9
<u>B. pennata</u> var. <u>secunda</u> (detached)	7.1	25.7	2.6	33.8	27.8	3.3	11.3
<u>Caulerpa racemosa</u> var. <u>uvifera</u>	3.9	8.0	0.7	61.4	24.6	6.3	6.3
<u>C. racemosa</u> var. <u>macrophyssa</u>	3.7	9.1	0.9	63.8	25.5	6.5	7.5

¹Reported on a dry matter basis as determined by the "proximate analysis" method commonly used for terrestrial animal forage.

²Present in benthic algae as a complex polysacchride; not true lignin or cellulose as found in terrestrial plants.

³Nitrogen x 6.25.

Table 11.--Mineral composition of principal food sources used by green turtles.¹

Algae	Ca	P	K	Mg	Na	Fe	Cu	Mn	Zn
	%					ppm			
<u>Bryopsis pennata</u> var. <u>secunda</u> (foraging site)	2.00	0.27	0.94	1.06	11.10	110	8	19	57
<u>B. pennata</u> var. <u>secunda</u> (detached)	1.82	0.23	0.93	0.95	10.00	88	10	17	66
<u>Caulerpa racemosa</u> var. <u>uvifera</u>	2.45	0.10	1.07	0.41	19.36	90	9	9	76
<u>C. racemosa</u> var. <u>macrophyssa</u>	0.87	0.10	1.28	0.31	22.00	2,558	11	29	81

¹Dry matter basis. Ca = Calcium; P = Phosphorus; K = Potassium; Mg = Magnesium; Na = Sodium; Fe = Iron; Cu = Copper; Mn = Manganese; Zn = Zinc.

Table 12.--Identification of epizootes sampled from green turtles.

Tag No.	Sex	Straight carapace length (cm)	Epizootes
7485	Female	95.9	<u>Acrochaetium</u> sp. <u>Polysiphonia taudana</u> <u>Lyngbya semiplena</u> Unidentified roundworms Unidentified amphipods Unidentified black "mites"
7565	Female	92.5	<u>Acrochaetium</u> sp. <u>Polysiphonia taudana</u> <u>L. semiplena</u> <u>Sphaecelaria tribuloides</u> <u>Urospora</u> sp. <u>Pilinia</u> sp. ¹ Unidentified foraminifera
7512	Male	89.0	<u>Acrochaetium</u> sp. <u>Polysiphonia taudana</u> <u>L. semiplena</u> <u>Urospora</u> sp. <u>Pilinia</u> sp. ¹ <u>Chadophora</u> sp. (trace) <u>Dermocarpa sphaerica</u> (epiphytic on <u>Chadophora</u> sp.)
7495	Female	82.9	Same as tag No. 7485
7481	Female	72.8	<u>Polysiphonia taudana</u> <u>L. semiplena</u> <u>Urospora</u> sp. <u>Pilinia</u> sp. ¹

¹Possibly Pilinia rimosa Kützting, which may be a new record for the tropical Pacific.

Table 13.--Red blood cell cholinesterase values for nine green turtles.

Tag No.	Straight carapace length (cm)	Weight (kg)	Net location	Sex ¹	Cholinesterase ²
7485	95.9	151.4	2	Female	0.15 0.16
7490	89.7	115.9	7	Male	0.27 0.27
7500	89.5	—	2	Female	0.13
7512	89.0	114.1	2	Male	0.23
7517	83.3	84.5	2	Male	0.29 0.30
7495	82.9	87.7	2	Female	0.14 0.13
7555	79.1	74.1	1	Male	0.32 0.34
7505	75.2	65.0	7	Female	0.26
7481	72.8	63.6	2	Female	0.28 0.31

¹Based on testosterone level.

²Decrease in pH units (pH/h) using a 0.2 ml aliquot.



Figure 1.--Location of turtle nets.

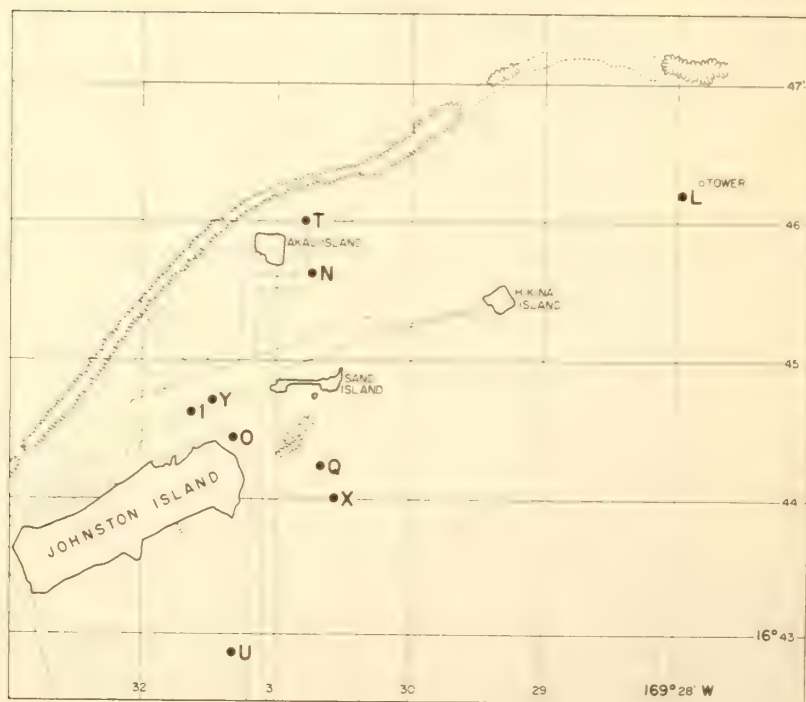


Figure 2.--Central location of 26 diving surveys with scuba. The bottom areas actually covered extend out in concentric circles from each location and overlap considerably for many dives.

ATOLL RESEARCH BULLETIN

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ENVIRONMENTAL SURVEY OF MATAIVA ATOLL,
TUAMOTU ARCHIPELAGO FRENCH POLYNESIA

By

B. DELESALLE AND COLLEAGUES

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In addition to the author's own research results, this paper includes contributions by many colleagues, from unpublished reports, theses in progress and other data, which are here gratefully acknowledged. These collaborators and their affiliations are listed below. All are also attached to the Centre de l'Environnement in Moorea⁽¹⁾.

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ENVIRONMENTAL SURVEY OF MATAIVA ATOLL, TUAMOTU ARCHIPELAGO FRENCH POLYNESIA

By

B. DELESALLE AND COLLEAGUES *

INTRODUCTION

Mataiva Atoll, one of 84 in French Polynesia, is a small coral island at the western edge of the Tuamotu Archipelago. This atoll occupies a particular place among the French Polynesian atolls since the discovery beneath the lagoon sediments of deposits of phosphates soon to be exploited. In order to estimate the environmental effects of such exploitation and plan a management scheme, numerous studies have been carried out since 1978 by many scientific organizations: Antenne du Muséum National et de l'Ecole Pratique des Hautes Etudes en Polynésie Française, Office de la Recherche Scientifique et Technique d'Outre-Mer (ORSTOM), B.C. Research, Institut de Recherches Médicales Louis Malardé (IRMLM), Centre National pour l'Exploitation des Océans (CNEXO) and Commissariat à l'Energie Atomique (CEA-LESE).

Because of the unusual and interesting results of these impact studies, the Antenne Museum-E.P.H.E. has, since 1981, continued the scientific survey of Mataiva Atoll. The geology and geomorphology of the atoll, the hydrological characteristics of lagoon waters and the abundance and diversity of the marine flora and fauna have been investigated by about 20 scientists. Several contributions, including for example studies of fishes, crustaceans and phytoplankton, are extracted from doctoral manuscripts.

Mataiva atoll has been chosen as the site of a post-Congress field trip of the Fifth International Coral Reef Congress, to be held in Tahiti in June 1985.

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Figure 1: Location of Mataiva atoll in French Polynesia and mosaic prepared from aerial photographs.



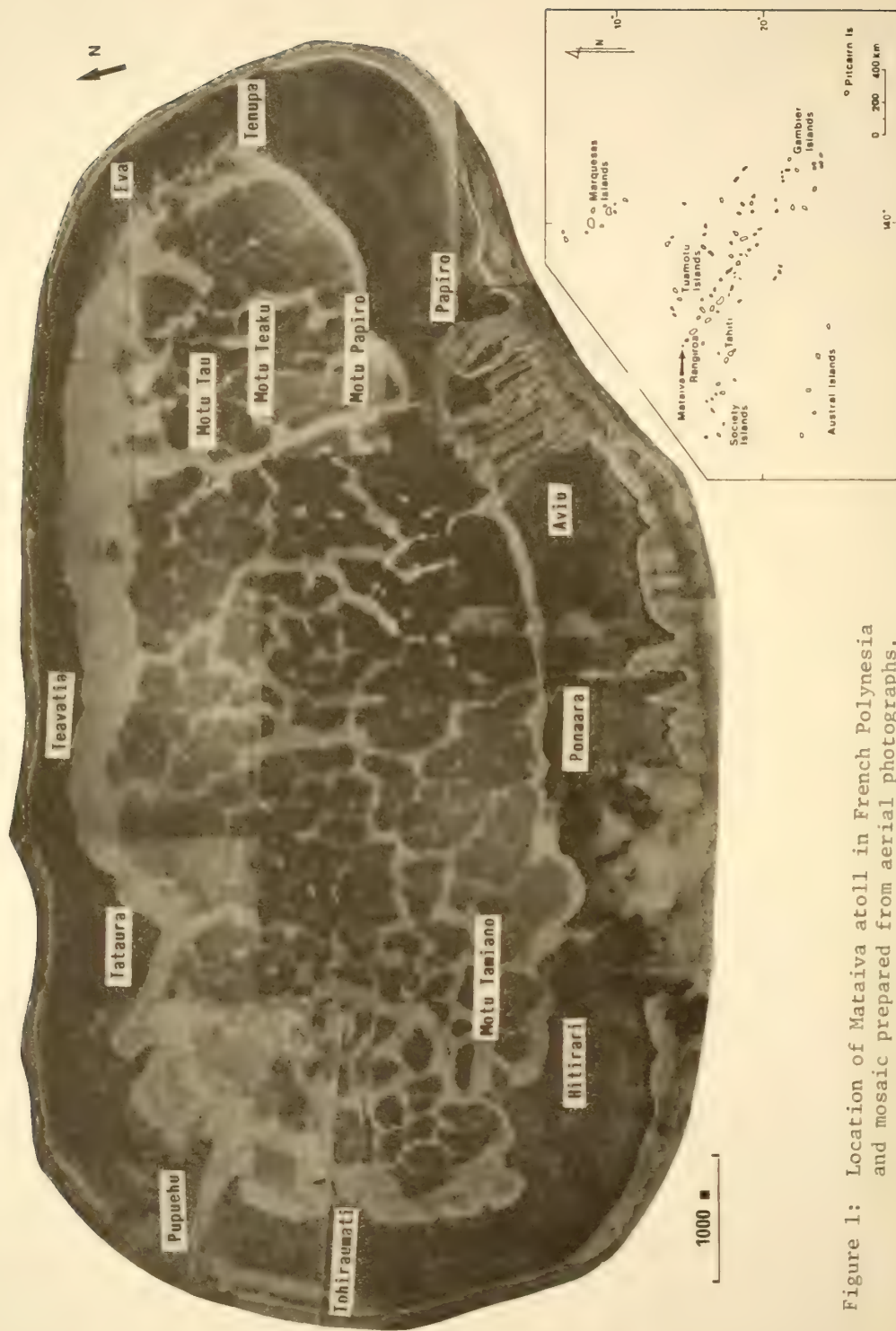


Figure 1: Location of Mataiva atoll in French Polynesia and mosaic prepared from aerial photographs.

PRESENTING MATAIVA ATOLL

Geography

Mataiva atoll is located 300 km north of Tahiti, $14^{\circ} 55'$ lat. S and $148^{\circ} 36'$ long. W. It is the westernmost atoll in the Tuamotu Archipelago. This small island, 10 by 5 km, is distinguished by its unusual morphology: a wide atoll rim, almost continuous, allowing only limited oceanic exchanges, and a reticulated lagoon divided into numerous basins by a network of slightly submerged partitions (Figure 1).

The climate is not unlike that elsewhere in Polynesia, i.e. tropical, hot and humid, with 2 seasons: one, relatively dry and cool ($24-27^{\circ}\text{C}$) from April to September, and the other, hot and rainy ($28-30^{\circ}\text{C}$) from October to March. Since the atoll has little relief, rainfall rarely exceeds 2.5 m per year, and the amount of sunshine is high (2500 hours per year). Storms and cyclones are rare with the exception of 1983, when 3 cyclones hit Mataiva. Trade winds are dominant, blowing from the eastern sector at an average speed of 7 to 10 m/s. The swell is generally less than 4 m, coming mainly from the South.

Background and population

Europeans discovered Mataiva in 1819: it was then named Lazareff Island by Bellingshausen. The numerous archeological discoveries bear witness to a more or less permanent pre-European settlement. Mataiva then belonged to the 8 independent kingdoms of the western Tuamotu, which formed the cultural and linguistic area of Mihiroa. However, this island was often uninhabited, particularly after its people were massacred in the 18th century by the inhabitants of Anaa atoll.

The present population on Mataiva is of recent origin. Around 1940, representatives from various families of the neighbouring atoll, Tikehau, who were exploiting Mataiva's copra, decided to settle there. The atoll was declared autonomous in 1950 and in 1971 was associated with the community of Rangiroa (Jarrige et al., 1978).

In 1983, the population of Mataiva numbered 183. It is a population of predominantly younger generation (55.8% are under 20 years old), slightly unbalanced (63.4% being female) and very fluctuating because of its proximity to Tahiti. The relationship, with Tikehau and Makatea, to the larger community of Rangiroa, explains the frequent population surges to these islands, whether temporary or permanent. For example, of the 172 persons established on Mataiva recorded in a survey taken in 1964 only 41 were still there in 1983.

Economy

Fishing and copra production are the two traditional means of support on the Tuamotu Atolls. These two natural resources are enough to insure the subsistence of the inhabitants and to allow the surplus to be commercially exploited. Being close to Tahiti, the main market, Mataiva

glories in its privileged position; moreover, it will be able to add the yield from the exploitation of phosphates to its future revenue.

Fishing. . On atolls generally, the sea provides about 70% of the proteins consumed, mainly through fish, but also sea food (shell fish and crustaceans) collected along the reef, and turtles which are considered a great delicacy. Fishing techniques vary: spears ("pupuhi"), rods ("aira"), lines or nets are used, but commercial fishes are above all collected in fish traps, then sold to passing schooners. These fish traps are located in the pass and next to the hoa (ocean-lagoon channels) and passively catch reef fishes. The amount of the catch varies greatly throughout the year and provides around 45 tons annually.

Copra. An essential atoll resource, copra occupies a large majority of the population throughout the whole year: the upkeep of the coconut grove, harvesting and drying of the nuts and the export to Tahiti. Due to the size of its emerged reef rim, Mataiva is an important producer with an annual harvest of nearly 450 tons, i.e. about 5% of the total production in the Tuamotu Archipelago. Unfortunately, this production was completely eliminated as a result of the 1983 cyclones and for at least two years, the main activity has been devoted to the restoration of the devastated coconut plantations.

Phosphates. The phosphate deposit represents the future--although at the moment hypothetical--wealth of Mataiva. It extends for approximately 5 km² and represents 15 millions tons of ore, 10 of which can be extracted. Its exploitation, forecast to last 10 to 15 years, will necessitate the employment of about 200 people. Such a project will result in complete upheaval in the atoll's morphology and the way of life for its inhabitants, but should not do so to the detriment of its traditional resources. One hopes that Mataiva will not experience the same fate as its neighbouring island, Makatea, which was practically deserted following the exploitation of its deposits.

GEOLOGICAL SETTING OF MATAIVA ATOLL

The morphological and sedimentological characteristics of Mataiva atoll are rather different from those encountered in most other atolls of French Polynesia. These singularities appear to be a consequence of unusual and late geological events which caused, among other things, the formation of a reticulated lagoon and deposits of exploitable phosphates. In particular, tectonic uplift of the NW Tuamotu atolls presumably resulted from the loading effects of the nearby volcanic complex. A crustal moat has developed peripheral to Tahiti, Moorea and Mehetia volcanoes. Beyond the outer edge of the moat, flexuring (buckling) has developed an arch which has been uplifted by about 10 meters (Pirazzoli and Montaggioni, in press).

Geomorphology of Mataiva

When approaching Mataiva by plane, one is immediately struck by 2 morphological characters: a wide reef rim and a partitioned lagoon.

The emerged reef ring is 200 to 1500 m wide, i.e. somewhat wider than found in the other atolls of the Tuamotu Archipelago. This reef rim is almost continuous, broken only by some channels (hoa) on its southern coast and a small atypical pass in the NW. The N and E coastlines form a single islet (motu).

A topographic cross-section (Figure 2) allows a proper understanding of this atoll's morphology. It reveals a marked dissymmetry between the N and S coasts of the atoll--the N and NE coasts are narrow (200-500 m) and of relatively high altitude (+ 6 m), whereas the southern coasts are lower and wider (1000-1500 m). In the same way, this asymmetry continues to the inner slope, which is wider (300 m) on the N coast than on the southern one (50 m). This dissymmetry is easily accounted for by the violent storms coming from the N with the resultant accumulation of storm ridges on the N coast, while the lagoon muds are transported southwards where they contribute to the supratidal accretion of the southern motu. This high energy sedimentation contrasts with that which prevails in a "normal" meteorological situation, where the influence of the S E tradewinds favours rather the widening of the northern inner slope.

The outer reef, of variable width (150-500 m), is characterised by 2 fundamental features :

- The presence of a reef flat flagstone, more or less eroded, located below and behind the algal ridge, where biotrititic sedimentation is weak or non-existent.
- The presence of an algal ridge in the process of chemical erosion; remnants of a raised, fossil ridge appear in some places; crusts of living coralline algae are spotty. Construction is quite inactive and the relief is in the process of degradation.

The lagoon morphology is the most original characteristic of Mataiva atoll. It is a reticulated or partitioned lagoon, made up of about 70 pools of varying sizes (100 m to over 2 km), with an average depth of 8 m. The shallows which separate these pools are under 0.1-0.8 m of water and form a network over 200 km long.

This sort of reticulated lagoon seems to be the only one in French Polynesia but its morphology is reminiscent of certain reef zones of Bora Bora (Society Archipelago) or of Ponape (Caroline Islands), which also consist of such lagoon pools each isolated from the others. Surveys conducted in the lagoon reveal that this reticulation seems directly related to paleotopography, most likely a pre-Pleistocene surface, buried under 10-15 m of present-Holocene sediments. This paleotopography influences the present topography and makes up the framework of the atoll's general morphology. However, Holocene coral remnants located 30-40 cm above mean lagoon level, determine the morphology of the lagoon coast and form some small islets in the eastern and southwestern parts of the lagoon.

Outer reefal and lagoonal sediments

Grain-size analyses of bottom surface samples have only been made on the fraction larger than 40 μ m. Two textural parameters (mean size, Mz

and sorting, S_o) have been graphically determined from the cumulative frequency curve. There appears to be a sharp difference between the reefal and lagoonal sediments (Figure 3). On the reef rim, the sediments are medium to coarse sands or granules ($M_z = 0.67-3.45$ mm), usually well sorted ($S_o = 0.76-0.91$), except in the western sector ($S_o = 2.18$). In all cases, fractions smaller than 0.5 mm do not exceed 25%. On the contrary, sediments in the lagoon are fine or very fine sands, to muddy sands (10-50% of fractions < 40 μ m), or to sandy silts (over 50% < 40 μ m). The sorting is usually good ($S_o = 0.28-1.48$). Higher percentages of silts have been found on the shoals sides or at the bottom of the basins, mainly in the N and E sectors of the atoll (50-80% of silts).

The composition of sediments reveals 2 main sources, corals and Corallinaceae. Green calcareous algae (Halimeda), Foraminifera and molluscs can also make up an important part of the sediment. Crustacea, serpulids, sponges and Bryozoa are also found. Figure 3 shows the grain size and composition of sediments in different parts of the outer reef and lagoon. The important features to emphasise are the abundance of Foraminifera on the southern outer reef, the great variation of percentages of Halimeda and Foraminifera in the lagoon, and the better representation of Corallinaceae and molluscs in the lagoon than on the outer reef.

Sequence of the main geological events at Mataiva atoll

Geological investigations by subsurface drilling showed the dominant influence of the pre-Holocene surfaces on the topography of Mataiva's reef structures. By reference to the geological history of other French Polynesian atolls and particularly that of Makatea (Montaggioni, 1985), the geological history of Mataiva can be summed up as follows :

During the Mio-Pliocene(?) a platform-like reef developed. This old reef is at present emerging along the N coast in the upper part of the ocean side beach. In the central and southern parts of the atoll, it is buried under a layer (a few to 30 m deep) of Holocene deposits. During several spells of emergence, this old reef underwent severe meteoritic solution and partial dolomitization.

During a later stage (Pliocene ?), the cavities of the karst thus formed were filled up with a phosphate deposit. The contrast in facies between the rocks of the old reef and the deposit demonstrates the totally different conditions of deposition for the phosphate. However, at present it is not possible to offer a reliable reconstruction of the deposition environment of the phosphates. Three alternatives may be proposed for their origin: on weakly consolidated carbonate rocks (high residual porosity), phosphorites may have been formed by (a) alteration and diagenesis of sea birds excrements and bones, (b) alteration of marine organic matter, deposited under low oxygen conditions, (c) post-depositional alteration of drift volcanic material that accumulated as soils.

Subsequent to phosphatogenesis, Mataiva Island underwent a slight tectonic uplift which appears to be confirmed by the absence of deposits linked to the 120,000 B.P. high sea level, which is found at Moruroa

atoll between 7 and 11 m below the Holocene deposits (Buigues, 1983).

The island was later submerged and thus the phosphate deposits and the rest of the old reef were recolonised by coral growth during the Holocene transgression, about 6,000 years ago.

Lastly, between 5,000 and 2,000 B.P., coral growth developed at Mataiva at a level slightly higher than the present one. The relicts of algal ridges found on the outer reef ($2,200 \pm 130$ yrs) and the Porites colonies of the lagoon motu ($5,210 \pm 130$ yrs) are at elevations similar to the emerged beachrocks, in which lithification patterns indicate an exposure patterns to vadose diagenetic environments during their formation (Montaggioni and Pirazzoli, 1984).

HYDROLOGICAL ENVIRONMENT

The hydrological characteristics of Mataiva atoll have a direct connection with 2 main morphological features: (1) a lagoon of reduced size and depth, whose shoals further restrict the volume (2) limited but still existing relations with the ocean through hoas and passes. Consequently, the physicochemical characteristics of the lagoon waters, if they show a certain spatial homogeneity, present an enormous temporal variability, principally dictated by climatic conditions (Delesalle, 1982).

Currents

The hoas' position, close together on the S side of the atoll and facing the dominant swells, in relation to that of the pass on the opposite sheltered coast, brings about a general circulation of the waters from the S towards the NW. Oceanic waters enter the lagoon through the hoas, whilst, in the pass, the current is most often outgoing (Figure 4).

In the lagoon, the partitions slow down considerably the water's circulation, and only the wind-induced currents are measurable. However, because of the larger size of the basins along the northern and southern coasts, the flow of water may preferentially follow them, and avoid the atoll's centre. In this case, the eastern part of the lagoon, isolated by a transversal string of islets, appears more confined.

Water level

The small amount of ocean-lagoon exchanges, added to the relatively reduced volume of the lagoon, explains how the water level can undergo considerable variations. An example of such variations, recorded daily since 1979 next to the pass, is given in Figure 5. Their usual amplitude is about a metre, but can reach or surpass 1.5 m when a very strong swell occurs. On the other hand, these variations are very rapid, a rise of 40 cm in 24 hours is not unusual. Considering the area of the lagoon (2500 ha), such an increase corresponds to an entry of water of about 10^7 m^3 , i.e. 1/10 of the lagoon volume. The lowering of this level is more gradual, around 10 cm in 24 h, but can last for periods of 7 to 10 days, and thus reach such a low level that the coral colonies on the top of the partitions emerge.

The general evolution of the level over 5 years shows a certain predominance of lower levels between July and December, but without well defined cycles.

The variations in the lagoon level show that Mataiva cannot be called a closed atoll. The existence of a pass, although atypical and shallow, guarantees permanent oceanic exchanges.

Temperature and salinity

Water temperatures in the lagoon do not vary much and generally follow the air temperatures with a maximum (29° - 31° C) in the rainy season and a minimum (25° - 27° C) during the dry season. If there is a slight warming up of the surface waters during the day, still a marked thermic stratification does not occur as could be expected in the absence of circulation.

This homogeneity of the water column is confirmed by salinity levels which differ little between surface and bottom. Temporal variations in salinity are more marked. In fact, if the lagoon waters near the hoa show salinity values usually close to those of the ocean (36 g/l), in the rest of the lagoon drops in salinity (30.77 to 33.89 g/l in April 1981) or increases (36.56 to 37.64 g/l in October 1983) can be observed.

If climatic conditions (heavy rains or long periods of dryness) directly influence the salinity of lagoon waters, the phreatic freshwater, held in the atoll foundation, also plays a role: the low salinity levels observed in April 1981 were measured after a month without noticeable precipitation while over 500 mm of rain had been recorded the month before.

Turbidity and light penetration

The lagoon waters of Mataiva always have a more or less pronounced milky appearance. Secchi disc measurements of water transparency reach 50 m in the ocean, but do not exceed 7 m in the lagoon near the hoa and 2.5 m near the pass. Quantum measurements indicate a quick absorption of light with depth (Figure 6). The attenuation coefficient deduced from these curves is weaker near the hoa (0.14) than towards the north of the lagoon (0.28); the most turbid waters (0.36) are found near the pass. However, the amount of suspended matter is not very great: 6.7 to 9 mg/l. This strong decrease in light in the water is caused by very fine, silty, calcareous particles.

Dissolved oxygen

Levels of dissolved oxygen vary very little (5.4 to 7 mm/l) and remain close to, or higher than the level of water saturation, depending on temperature and salinity. Such values indicate a confined environment where photosynthetic organisms play a major role in water oxygenation.

Nutrients

Lagoon waters of atolls are usually considered to be oligotrophic because of the absence of continental influences. Mataiva lagoon water, on the contrary, contains high and variable concentrations of dissolved nutrients, especially nitrates and silicates (0.10-13.99 $\mu\text{atg N-NO}_3/\text{l}$, 0.3-16.5 $\mu\text{atg Si/l}$). Heterogeneity is very marked between different areas of the lagoon and different periods of measurements, but no well-defined pattern can be recognized from the distribution of the values.

The confinement of the lagoon water, its lack of depth and its division into numerous pools, appear to be factors that allow such high and variable concentrations. Moreover, the migration of nutrients from the oceanic deep layers and the volcanic substratum through the coral foundation, as shown in Moruroa atoll (Rougerie et al., 1982) and in Takapoto atoll (Rougerie, 1983), might be an important contribution to the enrichment of the waters. Although we have no information about the porosity of the coral foundation of Mataiva, it is probably not less than on Takapoto considering the geological events (uplifts, karstification) undergone by Mataiva Atoll.

PRIMARY PRODUCERS OF MATAIVA LAGOON

Phytoplankton.

The phytoplankton of the lagoon waters is of relatively low specific diversity. Six classes of algae can be identified, Diatomophyceae, Dinophyceae, Chlorophyceae, Cyanophyceae, Cryptophyceae and Chrysophyceae (Coccolithophoridae), but with few species (Table A).

The diatoms dominate the phytoplanktonic flora by the diversity of the existing species, particularly the genera Mastogloia, typical of tropical seas, Nitzschia and Navicula. The scarcity of strictly planktonic forms such as Rhizosolenia, Chaetoceros or Thalassiosira must be noted. These are found only near the shore, where oceanic waters enter the lagoon. The populations are mainly made up of phytoplanktonic species. Dinoflagellates are also represented by species from calm and shallow environments: Gymnodinium, Gonyaulax and Prorocentrum (notably P. ovum). The other classes, especially Cryptophyceae and Chlorophyceae, are not often found in the plankton of atoll lagoons. The presence, and, at times the abundance, of some species such as the green alga Pyramimonas is a peculiar characteristic of Mataiva plankton.

The abundance of Mataiva's phytoplankton varies from 10^3 to $5 \cdot 10^5$ cells per litre. Quantitatively the small-sized phytoflagellates (10.30 μm) are often dominant while the diatoms are only locally abundant. A dinoflagellate Gymnodinium and a chlorophyceae Pyramimonas sometimes represent 90% of the cells counted.

The presence and importance of phytoflagellates in Mataiva plankton are characteristic of a calm and shallow environment. However, because of the richness in nutrients of the waters, one might expect a high

biomass in the plankton. On the contrary chlorophyll measurements give low values : 0.3 to 1 $\mu\text{g chl a l}^{-1}$ in surface waters, to 5 near the bottom. Nevertheless, the low percentage of degraded pigments (less than 35%) as well as the high level of primary production ($23-90 \text{ mg cm}^{-2} \text{ d}^{-1}$), so much higher than values usually observed in atolls (Sournia et Ricard, 1976; Delesalle et al. 1983), are indicative of a rapid turn-over in the phytoplanktonic populations. Such a paradox between low biomass and strong primary production can be partially explained by the wealth of zooplanktonic populations whose grazing can keep the phytoplanktonic biomass at a low level.

Benthic macroflora

The benthic macroflora in Mataiva's lagoon is characterised by a small number of species, of which only a few are abundant (Table B). Essentially, it is a hard substratum flora. Only a sea-grass, Halophila cf. ovalis, forms extensive grassbeds on the sandy shoals. A filamentous green alga, Enteromorpha, can also on occasion form large masses on the north inner slope.

Unlike high volcanic islands, where brown algae are the most abundant species, atoll floras are usually dominated by green and red algae. At Mataiva, the green algae are the most abundant and diversified (22 species), particularly the genera Caulerpa and Halimeda. One of them, Halimeda (opuntia group) is strongly developed on Mataiva, an unusual situation for an atoll lagoon. Among the Rhodophyceae, the crustose algae are more numerous in the lagoon and on the outer reef; however, gelidial turfs are well developed on the lagoon's dead corals and on the outer reef's flagstone. Cyanophyceae make up the 3rd class in the algal complement; if the usual extensive blue-green formations of atoll lagoon bottoms are not found in Mataiva, these algae do however form a discrete felt on dead corals and on Halophila leaves; their development is also important on beach edges, where they form an algal mat at times very thick, and in the brackish ponds of the atoll rim.

The distribution of algae in the lagoon is fairly homogeneous. Few species are present simultaneously. The specific diversity and abundance increase considerably near the zones of water exchange with the ocean (hoa and pass). On the outer reef flat, the eroded flagstone is covered with Gelidiales turf, while the brown alga Pocockiella variegata is dominant on its outer zone. Near the reef front, soft algae common to this zone (Microdictyon, Dyctiosphaeria cavernosa, Neomeris van bosse) appear, as well as crustose corallinaceae, Porolithon onkodes, Chevaliericrusta sp. But they never form an algal ridge typical of the reef front of an atoll, and their mass always remain poorly developed.

Thus, Mataiva's marine flora is that of a closed environment, with few species, some of which are abundant. It is homogeneous and gradually changes near the ocean exchange zones. Although not a rich flora, its vitality is demonstrated by the presence of numerous young shoots. The existence of large Halophila grassbeds and the unusual development of Halimeda (opuntia group) remain the distinctive characteristics of this flora.

MATAIVA LAGOON FAUNA

Zooplankton

The zooplankton of Mataiva atoll is mainly composed of typical, lagoonal holoplanktonic species where 6 species of Copepods, 2 species of Chaetognaths, 1 Appendicularia, 1 Ostracod and 1 Decapod Sergestid are dominant. Surprisingly, the meroplankton is extremely rare, 5% of the total plankton, whereas its true contribution is usually 35-65%. This meroplankton is made up of crustacean larvae (Stomatopods, Decapod Reptantia and Natantia), fish eggs and larvae, and Foraminifera. In other respects, while all of the Mataiva zooplankton species are recorded from other atolls, the absence of groups occurring in atolls open to the ocean, e.g. Pteropods, Salps, Doliolids and some Copepods, is noteworthy.

The zooplankton biomass is much higher than in the nearby ocean: 300-500 mg/m³ in the lagoon, 10-18 mg m⁻³ in the ocean.

The distribution of this biomass is very heterogeneous. Horizontally, the western and southern sectors of the atoll are about 3 times richer than the eastern and northern areas. Vertically, a very marked diurnal stratification exists between the surface (80 mg m⁻³) and the bottom (2 000 mg m⁻³) of the lagoon. This phenomenon has been observed in other atolls: Rangiroa (Michel, 1971), Mururoa (Michel, 1969), Takapoto (Renon, 1977), Bikini (Johnson, 1949).

The ocean-lagoon exchanges through the hoia and the pass are very important: entry of reef plankton, mainly meroplankton, and outpouring of lagoon plankton through the pass, in quantity about 35 times higher than what enters the lagoon. The lagoon thus constitutes an extremely productive environment, greatly enriching the nearby ocean.

The abundance and composition of Mataiva's zooplankton are somewhat unusual:

Firstly, its biomass is on the average 2 to 3 times greater than in other Polynesian atoll lagoons: 300 to 500 mg m⁻³ at Mataiva, 50 to 150 mg m⁻³ at Moruroa (Renon, unpubl.), 47 to 61 mg m⁻³ at Takapoto (Renon, 1977). The confinement of waters only partially explains this phenomenon, since Takapoto, a closed atoll, is poorer in zooplankton.

Secondly, the scarcity of meroplanktonic forms characteristic of Mataiva's zooplankton might be related to the depauperate benthic fauna, hence to lighter grazing and may account in part for a rich biomass.

Finally, the nutritional basis of zooplankton populations remains difficult to define. The phytoplankton biomasses are not in equilibrium with the zooplankton abundance, although the turnover rate of phytoplankton appears very high; however, the seston particles, which support bacterial development, may be directly used by the zooplankton.

Corals

As is often the case in closed atoll lagoons (Chevalier et Denizot, 1979), the specific diversity of Mataiva lagoon corals is especially low. Only 28 species have been recorded in the lagoon (Table C). The areas of maximum diversity (12-14 spp.) have been found at stations on the N and S coasts of the atoll. This relative variety is related to hydrodynamic conditions, due to the nearness of the hoā and the general flow of the water across the northern and southern edges of the lagoon. In fact, only those stations removed from the hoā and the pass have a low population.

The cover rate by scleractinians is generally very poor. The colonies are mainly located on the tops of the lagoon partitions, along the edges of the pools. Porites lobata, forming microatolls on the shoals, and Acropora tortuosa, more generally covering the pool sides, are the 2 most commonly reported species. Other species, Montipora aequituberculata and Leptastrea purpurea, are widely distributed, but form a poor cover because of the smallness of their colonies.

The coral fauna's vitality seems to be very poor and dead colonies are numerous. The percentage of living corals, which is almost 30% near the hoā but tapers to 0 in the eastern part of the atoll, is directly connected with hydrodynamic conditions. However, the size of the dead colonies of Porites and Acropora indicates an accidental origin for this condition. The combination of several environmental factors, such as a low water level along with much rain or intense sunshine, is likely to induce, in certain parts of the lagoon, hydrological conditions incompatible with coral survival, thus causing massive death.

The inhabitants of the atoll reported the occurrence of such an event in November 1978, repeated in November 1980: water level at 52 cm, extremely strong sunlight and water temperatures close to 32°C for 10 days. The lagoon waters turned green-brown in certain parts and produced a nauseating odour. In May 1981, the live coral cover was low throughout the lagoon, exceeding 10% only near the hoā. Other measurements taken in October 1983 show a considerable increase in live cover. Such a situation is only possible as a result of oceanic inflows, allowing recruitment of larvae and a return to conditions favouring the growth of the surviving species.

The outer reef coral fauna is much more diversified than that in the lagoon (Figure 10). These colonies are often small or very encrusting. The eroded reef flat flagstone is little colonised by corals which mainly develop near the reef front. Acropora and Pocillopora are the 2 best represented genera.

Molluscs

The malacological fauna of Mataiva, with 222 species recorded (Table D), is very unequally distributed between the lagoon and the outer reef.

On the outer reef, 169 species (156 gastropods and 13 bivalves) have been recorded. This fauna is fairly similar to those of other Tuamotu outer reefs. Nerita plicata, Nodolittorina leucosticta and Littorinaea

coccinea occupy the upper zone, where the scarcity of Tectarius grandinatus is rather surprising. The reef flat flagstone harbours nearly 30 species of which a large majority belongs to a carnivorous epifauna (Vasum, Conus, etc.). A wide variety of forms can be collected, although none is abundant except Cypraea moneta. The fauna of the forereef is dominated by Turbo setosus, actively exploited by the atoll's inhabitants. Live Drupa morum and Cypraea caput-serpentis are abundant there as well as numerous shells coming from the outer slope, evidence of its richness.

In the lagoon, 77 species have been collected: 55 gastropods and 22 bivalves. The species distribution is very uneven: the richest fauna occurs near the hoa in the S of the atoll. Here, the more abundant species belong₂ to the epifauna (Cypraeidae, Buccinidae): up to 20 Cyprea obvelata per m² under coral blocks; on the sandy shoals, Cypraea moneta is the only macromollusc found. One boring species, Lithophaga cinnamomina, inhabits the Porites colonies, at the rate of several dozen individuals per dm² of the living surface. There is also a difference between the windward and leeward coasts of the same reef: Arca ventricosa, Pinctada margaritifera and Tridacna maxima are more abundant on the leeward side.

Moving away from the S of the atoll, there is a considerable decline in the malacological fauna. The sandy shoals are occupied by a few Cardium fragrum beds. A small oyster, Crassostrea cucullata, is particularly abundant on the branches of dead Acropora. The endofauna of bottom sediments is also unusual, consisting of many species unknown elsewhere in French Polynesia.

Along the lagoon and motu edges, the malacological fauna shows little diversity, only 3 species being found there. The absence of the Nasses, Mitres, Cones and Terebres usually found in this zone is surprising.

On the littoral fringe of the motu, 3 species appear in succession: Littorina coccinea, Nerita plicata and Clypeomorus brevis, whilst the Cerithiidae and Cypraeidae usually present in the upper levels are absent. In the same way, the hoa contain an impoverished homogeneous mollusc fauna (8 species) which is characteristic of semifunctional hoa (functioning intermittently).

Mataiva's malacological fauna, which includes about 1/5 of the species recorded in French Polynesia (Richard, 1982), appears to be, on the whole, fairly rich. However, the lagoon fauna is, on the whole, poor, especially away from the zones under oceanic influence. Only a few species (Lithophaga cinnamomina, Crassostrea cucullata) are really very abundant. However, this malacological fauna is unusual because of the uncommon species found in the sediments and on the reef flats and the wide heterogeneity of the populations.

Crustacean fauna

The crustacean fauna of Mataiva atoll includes about 100 species (Monteforte, 1984). Most studies have been carried out on crabs,

especially coral-associated species, and on mud-shrimps, which are very numerous on the sandy shoals.

Crustacea inhabit all environments in Mataiva. Land crabs (Cardisoma carnifex) are plentiful in the coconut groves, as are hermit crabs Coenobita perlatus. The coconut crab Birgus latro, on the contrary, is rare (probably because of over-collecting).

The sandy environments of the lagoon are densely occupied by the mud-shrimps Callichirus armatus living in permanent burrows. Densities up to 3 mud-shrimps per square metre were observed on the muddy bottoms of the basins; they are lower in the shallow waters (0.5 to 1 ind./m²). For the whole lagoon, the estimated population of C. armatus ranges from 2.38 to 4.76 10⁷ individuals, i.e. a biomass of 285 to 571 tons wet weight (100 to 200 kg per hectare). Callichirus armatus is a great sediment reworker, feeding on the mud which falls into its gallery, and generating considerable disturbance. It has been estimated that the upper centimetre of mataiva's bottom sediment passes through the mud-shrimps' burrows 4 to 9 times per year. Living also in a burrow, the stomatopod Lysiosquilla maculata ("varo") is common and much prized because of its tasty flesh. A crab Calappa hepatica inhabits these sandy surfaces, being well adapted to this biotope. The hard substrates in the lagoon, and especially Porites microatolls, shelter a reduced fauna, dominated by 2 Xanthidae, Chlorodiella nigra and Phymodius unguatus, and 1 Portunidae, Thalamita admete, more numerous near the hoa.

The transition zones (hoa and pass) and the outer reef flats harbour a much more abundant and diversified population than does the lagoon. The hoa and the pass contain many species of the outer reef flat, which occasionally enter the lagoon: Chlorodiella cytherea, Liomera bella, Pilodius pugil. One also finds many juveniles of outer reef species: Etisus laevimanus, Thalamita and Leptodius. The Grapsidae and Paguridae are dominant in the slightly submerged zones.

On the outer reef flats, the fauna is equally abundant and diversified, particularly on the reef front (Table E). Many species, such as the crayfish, Palunirus penicillatus, climb the outer slope at night and are found on the crest. The exposure of the reef flat modifies the crustacean fauna and its distribution; thus, Plagusia speciosa is abundant on the whole exposed reef flat but less commonly found on sheltered reefs and there limited to the reef front.

On these outer reefs, the presence of living corals induces the existence of a well developed symbiotic fauna. This constitutes up to 80% of the individuals associated with a living coral. The Xanthidae among the Brachyura and the Alpheidae among the Natantia, are most abundant. In particular, crabs of the genus Trapezia (T. speciosa, T. bella and T. formosa) restricted to the coral Pocillopora, are particularly numerous in the frontal zones.

Other marine invertebrates

At present, only the major invertebrate groups have been studied. However, some interesting observations on other groups may be cited.

The sponges are abundant in the lagoon under the empty Tridacna shells or covering the dead Acropora branches. Many species with brightish colours are present, but the colonies are usually small, except for one black species, sometimes over 20 cm high, which is found in the lagoon and on the outer reef slope.

The echinoderms include few species but some of them are very abundant. Such is the case, in the lagoon, of the black sea-cucumber, Halodeima atra, with densities reaching 1 or 2 individuals per m^{-2} . This species is known to prefer more or less confined environments (Salvat, 1975; Salvat et al., 1979). Another sea cucumber, Cucumaria sp., is often found near the hoa under empty Tridacna shells.

On the outer reef, one may find two other Holothurians, the thin, long Synaptus near the beach, and the rounded, white spotted Bohadschia argus on the reef flat flagstone. But urchins are more abundant there. Echinometra mathaei is present in the reef flat cavities; near the reef front, the pencil urchin Heterocentrotus mamillatus is often found at the base of the spurs, while the helmet urchin, Colobocentrotus pedifer, whose morphology is well adapted to resist wave action, is more abundant on the upper part of the spurs, especially the relict algal ridge of the swell-exposed southern reef fronts.

Ascidians form very discrete colonies and are not well known in French Polynesia. However, symbiotic ascidians, associated with green algae (Prochloron), are present in Mataiva lagoon on the dead Acropora branches, and at the base of the spurs on the outer reef.

Fishes

The ichthyological fauna of Mataiva lagoon is poor, not only in number of species, but also in number of individuals. Of the 115 species recorded (Table F), only 10 seem well established in the lagoon and are in evidence at practically all the stations. These are usually small individuals belonging to the Gobiidae (Amblygobius phalaena, A. nocturnus), the Pomacentridae (Chromis coerulea), the Chaetodontidae (Chaetodon auriga, C. ephippium), or juveniles of Mullidae and Scaridae (Scarus sordidus, Scarus sp.). Some species, common to the lagoons of more or less closed atolls, are not found in Mataiva: Arothron hispidus, Chromis dimidiatus.

Near the hoa and the pass, the number of species reported increases considerably (40-52 species). Generally, there is much heterogeneity in the distribution and abundance of the fish populations of Mataiva lagoon. More detailed studies (Bell and Galzin 1984, Galzin 1985), carried out in 1981 and 1983, have demonstrated the close relation existing between the abundance and diversity of the fish fauna (total number of species, number of species $250 m^{-2}$, number of individuals $250 m^{-2}$) and the live coral cover. Changes in live coral cover, estimated to be as small as 0 to < 2% and < 2 to 2 to < 5%, produced significant increases in the total number of species and the number of individuals $250 m^{-2}$. On the other hand, the reef complexity, which is the same for dead and living coral colonies, is without any influence on fish populations.

In the pass and on the outer reef flats, the ichthyological fauna is much richer and made up of numerous species from the outside but which do not pass into the lagoon, such as triggerfishes (Balistoides undulatus, Pseudobalistes falmarginatus), jacks (Caranx trifasciatus), emperors (Lethrinus mahsena), goatfishes (Mugil angeli, M. vaigiensis).

On the outer slopes, the fish population is dominated by the Acanthuridae family, mainly Naso and Acanthurus. Pomacentridae, Serranidae, Lutjanidae and Chaetodontidae are equally abundant. The specific richness is at its maximum between 10 and 20 m (70 species), whereas the maximum abundance is found between 3 and 10 m. The effect of the 1983 cyclones on the outer reefs, causing massive coral destruction, has brought about a slight decrease of the herbivorous populations, but, above all, a redistribution of certain species and a much higher density in the upper levels of 3 to 10 m.

CONCLUSIONS

Mataiva atoll has a singular morphology whose major characteristic is the partitioning of the lagoon into numerous pools. This is due to its peculiar geological history, during which several periods of uplift and subsidence occurred. During the periods of emergence, erosion processes resulted in the formation of a karstic relief, in the cavities of which phosphate deposits accumulated.

The present morphology, moulded onto the former one, has, as a consequence, created particular hydrological conditions in the lagoon: very high turbidity, considerable variations in water level, high nutrient concentrations.

The biological communities of the lagoon show the characteristics of a closed environment: few species are present, but some are very abundant. Mataiva stands out among atolls because of its high level of primary production, abundant zooplankton and a fairly poor, but very uneven distributed, benthic macrofauna. This latter, subject to strong variations in hydrological conditions, can suffer enormous mortality levels, affecting especially the corals. However, the evolution observed since 1981 seems to indicate that this is an accidental phenomenon and that the lagoon's biological communities retain the capability to survive and grow under difficult conditions.

Future research on Mataiva atoll must take into account the wide range of variation in the distribution and abundance of its lagoonal populations. This fact seems to be closely related to the hydrological environment and its long-term variations. Such research will mainly concern the hydrology, the primary producers and a quantitative evaluation of the benthic and ichthyological fauna.

Although Mataiva seems to be a very special atoll whose characteristics cannot be used as a model for the other Tuamotu atolls, it is a very interesting experimental field for some ecological studies, e.g. the relationship between live coral cover and reef fish populations. A fish survey, similar to those made in 1981 and 1983, is already planned for mid-1985, to follow the changes in the fish communities, as the

In the pass and on the outer reef flats, the ichthyological fauna is much richer and made up of numerous species from the outside but which do not pass into the lagoon, such as trigger fishes (Balistoides undulatus, Pseudobalistes falmarginatus), jacks (Caranx trifasciatus), emperors (Lethrinus mahsena), goatfishes (Mugil angeli, M. vaigiensis).

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REFERENCES

- BELL, J.D., GALZIN, R., 1984 - Influence of live coral cover on coral-reef fish communities. **Mar. Ecol. Prog. Ser.**, 15 : 265-274.
- BUIGUES, D., 1983 - Sédimentation et diagenèse des formations carbonatées de l'atoll de Mururoa (Polynésie Française). **Thèse**, Univ. Paris X, 2 vol., 309 p.
- BOURROUILH - LE JAN, F., 1980 - Phosphates, sols bauxitiques et karsts dolomitiques du Centre et du Sud-Ouest Pacifique. **Doc. BRGM**, 24 : 113-128.
- CHEVALIER, J.P., DENIZOT, M., 1979 - Les organismes constructeurs du lagon de Takapoto. **J. Soc. Oceanistes**, 35(65) : 31-34.
- DELESALLE, B., 1982 - Un atoll et ses problèmes : Mataiva et ses phosphates. **Oceanis**, 8(4) : 329-337.
- DELESALLE, B., BAGNIS, R., BENNETT, J., BELL, J., DENIZOT, M., GALZIN, R., MONTAGGIONI, L., PAYRI, C., RENON, J.P., RICARD, M., VERGONZANNE, G., 1983 - Biology, hydrology and geomorphology of the atoll of Mataiva (Tuamotu Archipelago, French Polynesia). **15th Pacif. Sci. Ass. Cong.**, Dunedin, 1983, Abst. : 59.
- GALZIN, R., 1985 - Ecologie des poissons récifaux de Polynésie Française. **Thèse**, Univ. Montpellier, 195 p.
- HARMELIN-VIVIEN, M., LABOUTE, P., 1983 - Preliminary data on underwater effects of cyclones on the outer slopes of Tikehau island (Tuamotu, French Polynesia) and its fish fauna. **3rd Intern. Soc. Reef Stud. Symp.**, Nice, 1983, Abst. : 26.
- JARRIGE, F., GUEREDRAT, J.A., RECY, M., RAVAUULT, P., 1978 - Etude de l'atoll de Mataiva. **Rapport interne**, 62 p.
- JOHNSON, M.W., 1954 - Plankton of the northern Marshall Islands. **U.S. Geol. Surv. Prof. Papers**, 260 : 301-314.
- MICHEL, A., 1969 - Plankton du lagon et des abords extérieurs de l'atoll de Mururoa. **Cah. Pacif.** 13 : 81-132.
- MICHEL, A., COLIN, C., DESROSIERES, R., OUDOT, C., 1971 - Observations sur l'hydrologie et le plancton des abords et de la zone des passes de l'atoll de Rangiroa (Archipel des Tuamotu, Pacifique central). **Cah. O.R.S.T.O.M.**, sér. **Océanogr.**, 9 : 375-402.
- MONTAGGIONI, L.F., 1985 - Makatea island, Tuamotu archipelago. In : B.DELESALLE, R.GALZIN & B.SALVAT (Eds). **5th International Coral Reef Congress**, Tahiti 27 May - 1 June. Vol.1 : "French Polynesian Coral reefs": 103-158.
- MONTAGGIONI, L.F., PIRAZZOLI, P.A., 1984 - The significance of exposed coral conglomerates from French Polynesia (Pacific Ocean) as indicators of recent relative sea-level changes. **Coral Reefs**, 3 : 29-42
- MONTEFORTE, M., 1984 - Etude des peuplements de Crustacés Décapodes Reptantia et Stomatopodes de Polynésie Française. **Thèse**, Paris VI, 148 p.
- PIRAZZOLI, P. A., MONTAGGIONI, L. F., Geological factors controlling reef evolution in the north-western Tuamotu region. **Quaternary Research**, in press.
- RENON, J.P., 1977 - Zooplankton du lagon de Takapoto (Polynésie Française). **Ann. Inst. Oceanogr.** 53 : 217-236.

- RICHARD, G., 1982 - Mollusques lagunaires et récifaux de Polynésie Française : inventaire faunistique, bionomie, bilan quantitatif, croissance, production. **Thèse**, Paris VI, 313 p.
- ROUGERIE, F., 1983 - Nouvelles données sur le fonctionnement interne des lagons d'atoll. **C. R. Acad. Sc. Paris**, Série II, t. 297 : 909-912.
- ROUGERIE, F., RICARD, M., MAZAURY, E., 1982 - Le lagon de l'atoll de Mururoa. **Rapport C.E.A.**, R. 5236 : 92 p.
- SALVAT, B., 1975 - Qualitative and quantitative study of Halodeima atra, (Echinodermata, Holothuridea), in the lagoons and reefs of French Polynesia. **Proc. 13th Pacif. Sci. Cong.**, Vancouver, 1975. Abstr. 1 : 132.
- SALVAT, B., VERGONZANNE, G., GALZIN, R., RICHARD, G., CHEVALIER, J.P., RICARD, M., RENAUD-MORNANT, J., 1979 - Conséquences écologiques des activités d'une zone d'extraction de sable corallien dans le lagon de Moorea (île de la Société, Polynésie Française). **Cah. Indo-Pacif.**, 1(1): 83-126.
- SOURNIA, A., RICARD, M., 1976 - Données sur l'hydrologie et la productivité du lagon d'un atoll fermé (Takapoto, Iles Tuamotu). **Vie et Milieu** 26(2), Serie B : 243-279.
- VAUGELAS, J. de, 1983 - First record of the Callianassa (Crustacea, Thalassinidea) Callichirus armatus Milne-Edward 1870, in Polynesian Islands (Tahiti, Moorea and Mataiva). **3rd Int. Soc. reef Stud. Symp.**, Nice, Abstr. :23.
- VAUGELAS J. de, DELESALLE, B., MONIER, C., - Aspects of the biology of Callichirus armatus, A. Milne Edwards 1870 (Crustacea, Thalassinidea) from French Polynesia. **Crustaceana**, in press.

Table A : Distribution of the phytoplanktonic species in the different sectors of the lagoon.

	East	North	Pass	Hoia	Center
DIATOMOPHYCEAE					
Achnanthes sp.			x		
Actinopterychus undulatus		x		x	x
Amphiprora alata		x	x	x	
Amphora bigibba		x	x		x
Amphora exsecta	x	x	x	x	
Amphora obtusa		x			
Amphora ostrearia		x	x		
Amphora robusta			x		
Amphora sp.		x	x	x	x
Asterionella kariana				x	
Asterolampra marylandica					x
Biddulphia sp.					x
Caloneis liber		x			
Caloneis sp.		x	x		
Campylodiscus innominatus		x	x	x	
Chaetoceros sp.					x
Climacosphenia moniligera	x			x	x
Cocconeis sp.		x			x
C. placentula var. euglypta	x				
Coscinodiscus cf. eccentricus	x			x	x
Coscinodiscus radiatus				x	
Cyclotella meneghiniana		x			
Diploneis bombus			x		
Hemidiscus cuneiformis		x		x	
Grammatophora marina			x		
Gyrosigma corallinum	x				
Gyrosigma sp.		x	x		
Lymnophora Ehrenbergii		x	x	x	
Mastogloia affirmata	x				
Mastogloia binotata	x		x	x	x
Mastogloia corsicana		x	x		
Mastogloia decussata		x			
Mastogloia erythraea		x	x		
Mastogloia fimbriata		x	x		x
Mastogloia horvathiana	x	x	x		
Mastogloia oculata		x			x
Mastogloia ovata				x	
Mastogloia ovulum	x	x	x		
Mastogloia cf. pseudoparadoxa		x			
Mastogloia splendida		x			
Mastogloia cf. tenuis		x			
Mastogloia sp.			x		
Navicula exigua				x	
Navicula granulata		x			
Navicula longa			x		
Navicula lyra		x	x		

	East	North	Pass	Hoia	Center
Navicula cf menisculus		x	x		
Navicula perobesa	x		x	x	
Navicula sp.			x	x	
Nitzschia acuta	x	x		x	
Nitzschia closterium		x	x	x	x
Nitzschia distans		x			
Nitzschia longissima		x	x	x	x
N. punctata var coarctata			x		x
Nitzschia sigma			x		
Nitzschia seriata				x	
Nitzschia ventricosa		x			
Nitzschia sp.		x			x
Plagiogramma atomus				x	
Pleurosigma sp.		x		x	
Podocystis spathulata	x	x	x	x	x
Rhabdonema adriaticum		x			
Rhizosolenia sp.			x	x	
Stauroneis salina	x		x		
Surirella fastuosa	x	x		x	
Surirella reniformis	x	x			
Surirella sp.	x				
Synedra ulna			x	x	x
Synedra undulata	x	x			x
Thalassiosira sp.					x
Trachyneis sp.				x	
Triceratium shadboltianum				x	
Tropidoneis lepidoptera	x	x	x	x	
DINOPHYCEAE					
Ceratium pentagonum				x	
Dinophysis sp.					x
Exuviella sp.			x	x	
Gonyaulax spinifera		x			x
Gymnodinium splendens					x
Gymnodinium sp.	x	x	x	x	x
Oxytoxum sp.		x	x		
Ornithocercus quadratus				x	
Oxytoxum sp.					x
Prorocentrum sp.			x		
Protoperidinium sp.		x	x		
CHLOROPHYCEAE					
Carteria sp.	x	x	x	x	
Chlamydomonas sp.	x	x			
Nephroselmis sp.		x	x		
Pyramimonas sp.	x	x	x	x	x
CYANOPHYCEAE					
Oscillatoria sp.	x	x	x		
Pseudanabaena sp.			x	x	
Spirulina sp.		x	x	x	
CRYPTOPHYCEAE	x	x			x
COCCOLITHOPHORACEAE	x			x	x

Table B: Distribution of the main algal species in the lagoon and the outer reef.

	Outer Reef	Hoa	Pass	Lagoon East	North	Center
CYANOPHYCEAE						
Calothrix sp.		x	x	x		x
Hassalia byssoides	x	x				
Lyngbia majuscula			x			
CHRYSOPHYCEAE						
Chrysonephros sp.		x	x			x
PHEOPHYCEAE						
Dictyota sp.			x			
Lobophora variegata	x		x			
Sphacelaria furcigera		x				x
Sph. tribuloides		x				
Turbinaria ornata	x					
CHLOROPHYCEAE						
Acetabularia moebii			x			
Avrainvillea lacerata	x	x	x	x	x	x
Boodlea sp.		x	x			
Bryopsis sp.		x	x			
Caulerpa peltata		x	x			x
Caulerpa racemosa	x		x			
Caulerpa serrulata	x	x	x		x	x
Caulerpa sp.	x			x		x
Codium adherens		x				
Dictyosphaeria sp.	x	x	x	x	x	
Enteromorpha sp.		x	x			
Halimeda discoidea	x					
Halimeda opuntia	x	x	x	x	x	x
Microdictyon sp.	x	x				
Neomeris sp.	x					
Struvea elegans			x			
Trichosolen sp.		x				
RHODOPHYCEAE						
Centroceras clavulatum		x	x			
Ceramium tenerrimum		x	x			
Ceramium sp.		x	x			
Chevaliericrusta sp.	x					
Gelidium crinale	x	x	x		x	
Gelidium pusillum	x	x	x			
Herposiphonia secunda		x	x	x	x	
Hypnea sp.		x	x			
Jania sp.	x	x	x			
Liagora decussata	x					
Porolithon onkodes	x					
Porolithon craspedium	x					
Polysiphonia sp.		x	x		x	
Pterocladia media	x	x			x	

	OUTER REEF	PASS	LAGOON			
			NORTH (J)	SOUTH (B) (L)	CENTER (G)	EAST (C)
PSAMMOCORA CONTIGUA	+	+		+	+	
PSAMMOCORA SUPERFICIALIS	+					
POCILLOPORA DAMICORNIS	+					
POCILLOPORA EYDOUXI	+					
POCILLOPORA VERRUCOSA	+					
ASTREOPORA MYRIOPHTHALMA	+	+			+	
MONTIPORA AEQUITUBERCULATA			+	+		
MONTIPORA COMPOSITA	+		+	+		
MONTIPORA EDWARDSI				+		
MONTIPORA INFORMIS	+					
MONTIPORA TUBERCULOSA	+	+		+		
MONTIPORA TURGESCENS				+		
MONTIPORA VERRUCOSA			+	+		
ACROPORA DANAI	+					
ACROPORA HUMILIS	+		+			
ACROPORA LATISTELLA			+			
ACROPORA ROBUSTA	+					
ACROPORA TORTUOSA				+	°	°
ACROPORA VALIDA			+	+		
PAVONA MINUTA	+					
PACHYSERIS SPECIOSA	+					
FUNGIA FUNGITES	+					
PORITES (SYNARAEA) CONVEXA			+	+		
PORITES (NAPOPORA) IRREGULARIS	+			+		
PORITES LICHEN	+					
PORITES LOBATA	+	+	+	+	+	+
PORITES CF SOLIDA			+			
FAVIA PALLIDA			+			+
FAVIA ROTUMANA	+			+		
FAVIA STELLIGERA	+					
LEPTASTREA PURPUREA	+	+	+	+	+	+
LEPTASTREA TRANSVERSA				+		
CYPHASTREA SERAILA			+	+	+	+
PLATYGYRA DAEDALEA			+	+		
MONTASTREA CURTA	+					
ACANTHASTREA ECHINATA			+	+		
LOBOPHYLLIA CORYMBOSA	+					
° Dead Colonies						

Table C : Distribution of the main species of Scleractinians on the outer reef and in the lagoon.

Table D: List of Molluscs catalogued in the lagoon and on the outer reef

CLASS GASTROPODA**SUB-CLASS PROSOBRANCHIA****Order Archaeogastropoda****HALIOTIDAE***Haliotis pulcherrima* Gmelin, 1791**PATELLIDAE***Patella flexuosa* Quoy & Gaimard, 1834**STOMATELLIDAE***Stomatella sanguinea* (Adams, 1850)*Stomatella varia* (Adams, 1850)**TURBINIDAE***Turbo argyrostomus* Linné, 1758*Turbo petholatus* Linné, 1758*Turbo setosus* Gmelin, 1791**NERITIDAE***Clithon chlorostoma* (Broderip, 1832)*Nerita plicata* Linné, 1758*Puperita reticulata* (Sowerby, 1832)**Order Mesogastropoda****NEOCYCLOTIDAE***Amphicyclotus* sp.**LITTORINIDAE***Littorina coccinea* (Gmelin, 1791)*Nodilittorina leucosticta* (Reeve, 1857)*Tectarius grandinatus* (Gmelin, 1791)**TRUNCATELLIDAE***Truncatella* sp.**VERMETIDAE***Dendropoma maximum* (Sowerby, 1825)*Serpulorbis* sp.**PLANAXIDAE***Planaxis lineatus* (Da Costa, 1776)**MODULIDAE***Modulus tectum* (Gmelin, 1791)**CERITHIDAE***Bittium* cf. *glareosum* (Gould, 1861)*Bittium zebrum* (Kiener, 1841)*Cerithium atromarginatum* Dautzenberg & Bouge, 1933*Cerithium columna* Sowerby, 1834*Cerithium mutatum* Sowerby, 1834*Cerithium nesioticum* Pilsbry & Vanatta, 1906*Cerithium rostratum* Sowerby, 1855*Cerithium salebrosum* Sowerby, 1855*Clypeomorus brevis* Quoy & Gaimard, 1834*Clypeomorus moniliferus* (Kiener, 1841)*Rhinoclavis diadema* Houbrick, 1878*Rhinoclavis sinensis* (Gmelin, 1791)

EULIMIDAE

Eulima sp.

STROMBIDAE

Strombus dentatus Linné, 1758

Strombus gibberulus Linné, 1758

Strombus maculatus Sowerby, 1842

Strombus mutabilis Swainson, 1821

CALYPTRAEIDAE

Cheila equestris (Linné, 1758)

TRIVIIDAE

Trivia sp.

CYPRAEIDAE

Cypraea caputserpentis Linné, 1758

Cypraea carneola var. propinqua Garrett, 1879

Cypraea cumingii Sowerby, 1832

Cypraea depressa Gray, 1824

Cypraea dillwyni Schilder, 1922

Cypraea erosa Linné, 1758

Cypraea fimbriata Gmelin, 1791

Cypraea goodalli Sowerby, 1832

Cypraea helvola Linné, 1758

Cypraea irrorata Gray, 1828

Cypraea isabella Linné, 1758

Cypraea leviathan Schilder & Schilder, 1937

Cypraea maculifera (Schilder, 1932)

Cypraea margarita Dillwyn, 1817

Cypraea minoridens Melvill, 1901

Cypraea moneta Linné, 1758

Cypraea nucleus Linné, 1758

Cypraea obvelata Lamarck, 1810

Cypraea poraria Linné, 1758

Cypraea schilderorum (Iredale, 1939)

Cypraea scurra Gmelin, 1791

Cypraea serrulifera Schilder & Schilder, 1938

Cypraea subteres Weinkauff, 1880

Cypraea talpa Linné, 1758

Cypraea tigris Linné, 1758

Cypraea ventriculus Lamarck, 1810

NATICIDAE

Natica galteriana Recluz, 1844

Polinices melanostoma (Gmelin, 1791)

CYMATIDAE

Cymatium gemmatum (Reeve, 1844)

Cymatium hepaticum (Röding, 1798)

Cymatium muricinum (Röding, 1798)

Cymatium nicobaricum (Röding, 1798)

Cymatium rubeculum (Linné, 1758)

Distortio anus (Linné, 1767)

Gyrineum roseum (Reeve, 1844)

BURSIDAE

- Bursa bufonia (Gmelin, 1791)
- Bursa granularis (Röding, 1798)

COLUBRARIIDAE

- Colubraria nitidula (Sowerby, 1833)
- Colubraria tortuosa (Reeve, 1844)
- Colubraria sp.

Order Neogastropoda

MURICIDAE

- Drupa clathrata (Lamarck, 1816)
- Drupa grossularia Röding, 1798
- Drupa morum (Röding, 1798)
- Drupa ricinus (Linné, 1758)
- Drupa speciosa (Dunker, 1867)
- Drupella cornus (Röding, 1798)
- Drupella fenestrata (Blainville, 1832)
- Drupella ochrostoma (Blainville, 1832)
- Homalocantha martineta (Röding, 1798)
- Maculotriton seriale (Deshayes, 1834)
- Mancinella tuberosa (Röding, 1798)
- Morula granulata (Duclos, 1832)
- Morula margariticola (Broderip, 1832)
- Morula uva (Röding, 1798)
- Nassa francolinus (Bruguière, 1789)
- Pterinotus loebbeckei (Kobelt, 1879)
- Thaïs aculeatus (Deshayes & Milne-Edwards, 1844)
- Thaïs armigera (Link, 1807)

CORALLIOPHILIDAE

- Coralliophila cf. porphyroleuca (Crosse 1870)
- Coralliophila violacea (Kiener, 1836)
- Leptochoncus lamarcki Deshayes, 1863
- Quoyula madreporarum (Sowerby, 1832)

BUCCINIDAE

- Cantharus fumosus (Dillwyn, 1817)
- Cantharus spica (Melvill & Standen, 1895)
- Cantharus undosus (Linné, 1758)
- Engina incarnata (Deshayes, 1834)
- Engina sp.
- Pisania decollata (Sowerby, 1833)
- Pisania ignea (Gmelin, 1791)
- Pisania iostoma (Gray, 1834)
- Pisania truncata (Hinds, 1844)

COLLUMBELLIDAE

- Mitrella sp.
- Pyrene flava (Bruguière, 1789)
- Pyrene scripta (Lamarck, 1822)

NASSARIIDAE

- Nassarius gaudiosus (Hinds, 1844)
- Nassarius cf. pauperus (Gould, 1850)

FASCIOLARIIDAE

- Latirus sanguifluus* (Reeve, 1847)
Latirus sp.
Peristernia chlorostoma (Sowerby, 1825)
Peristernia nassatula (Lamarck, 1822)
Peristernia sp.

VASIDAE

- Vasum ceramicum* (Linné, 1758)

HARPIDAE

- Harpa gracilis* Broderip & Sowerby, 1829

MITRIDAE

- Imbricaria punctata* (Swainson, 1821)
Mitra assimilis Pease, 1868
Mitra coffea Schubert & Wagner, 1829
Mitra columbelliformis Kiener, 1838
Mitra cucumerina Lamarck, 1811
Mitra fastigium Reeve, 1845
Mitra ferruginea Lamarck, 1811
Mitra litterata Lamarck, 1811
Mitra paupercula (Linné, 1758)
Mitra pellisserpentis Reeve, 1844
Mitra stictica (Link, 1807)

COSTELLARIIDAE

- Thala mirifica* (Reeve, 1845)
Thala sp.
Vexillum cadaverosum (Reeve, 1844)
Vexillum crocatum (Lamarck, 1811)
Vexillum cumingii (Reeve, 1844)
Vexillum speciosum (Reeve, 1844)

TURRIDAE

- Clavus formosus* (Reeve, 1847)
Daphnella sp.
Lienardia rubida (Hinds, 1844)
Lienardia cf. *roseotincta* (Montrouzier, 1872)
Xenuroturris cingulifera (Reeve, 1847)

CONIDAE

- Conus auratinus* Da Motta, 1982
Conus auricomus Hwass in Bruguière, 1792
Conus catus Hwass in Bruguière, 1792
Conus chaldaeus (Röding, 1798)
Conus cylindraceus Broderip & Sowerby, 1830
Conus distans Hwass in Bruguière, 1792
Conus ebraeus (Linné, 1758)
Conus flavidus Lamarck, 1810
Conus geographus Linné, 1758
Conus legatus Lamarck, 1810
Conus lividus Hwass in Bruguière, 1792
Conus magnificus Reeve, 1843
Conus miles Linné, 1758
Conus miliaris Hwass in Bruguière, 1792
Conus pertusus Hwass in Bruguière, 1792

Conus pulicarius Hwass in Bruguière, 1792
Conus rattus Hwass in Bruguière, 1792
Conus retifer Menke, 1829
Conus scabriusculus Dillwyn, 1817
Conus sponsalis Hwass in Bruguière, 1792
Conus tenuistriatus Sowerby, 1858
Conus textilinus Kiener, 1845
Conus tulipa Linné, 1758
Conus vexillum Gmelin, 1791

TEREBRIDAE

Terebra crenulata (Linné, 1758)
Terebra guttata (Roding, 1798)

Order Heterogastropoda

ARCHITECTONICIDAE

Heliachus infundibuliformis (Gmelin, 1791)

EPITONIIDAE

Epitonium sp.

JANTHINIDAE

Janthina ianthina (Linné, 1758)

TRIPHORIDAE

Triphora sp.

SUB-CLASS OPISTHOBRANCHIA

Order Entomotaeniata

PYRAMIDELLIDAE

Pyramidella sp.

Order Cephalaspidea

ACTEONIDAE

Pupa solidula (Linné, 1758)

HYDATINIDAE

Hydatina amplustre (Linné, 1758)

ATYIDAE

Atys sp.

SUB-CLASS PULMONATA

Order Basommatophora

ELOBIIDAE

Melampus sp.

CLASS BIVALVIA

Order Arcoida

ARCIDAE

Arca imbricata Bruguière, 1789
Arca ventricosa Lamarck, 1819

Order Mytiloida

MYTILIDAE

Lithophaga cinnamomina (Chemnitz, 1785)
Modiolus auriculatus Krauss, 1848

PINNIDAE

Pinna muricata Linné, 1758

PTERIIDAE

Pinctada maculata (Gould, 1850)
Pinctada margaritifera (Linné, 1758)

ISOGNOMONIDAE

Isognomon sp.

PECTINIDAE

Chlamys inaequalis (Sowerby, 1842)

Chlamys sp.

OSTREIDAE

Crassostrea cucullata (Born, 1778)

Order Hippuritoida

CHAMIDAE

Chama iostoma Conrad, 1837

Chama pacifica Broderip, 1834

Order Veneroida

LUCINIDAE

Anodontia edentula (Linné, 1758)

Codakia punctata (Linné, 1758)

Codakia divergens (Philippi, 1850)

CARDIIDAE

Corculum fragum (Linné, 1758)

TRIDACNIDAE

Tridacna maxima (Röding, 1798)

TELLINIDAE

Arcopagia robusta (Hanley, 1844)

Quidnipagus palatam Iredale, 1929

Scutarcopagia scobinata (Linné, 1758)

Tellina donaciformis Deshayes, 1854

Tellina obliquaria Deshayes, 1854

PSAMMOBIIDAE

Asaphis violaceus (Forskål, 1775)

TRAPEZIIDAE

Trapezium oblongum (Linné, 1758)

VENERIDAE

Gafrarium pectinatum (Linné, 1758)

Pitar prora (Conrad, 1837)

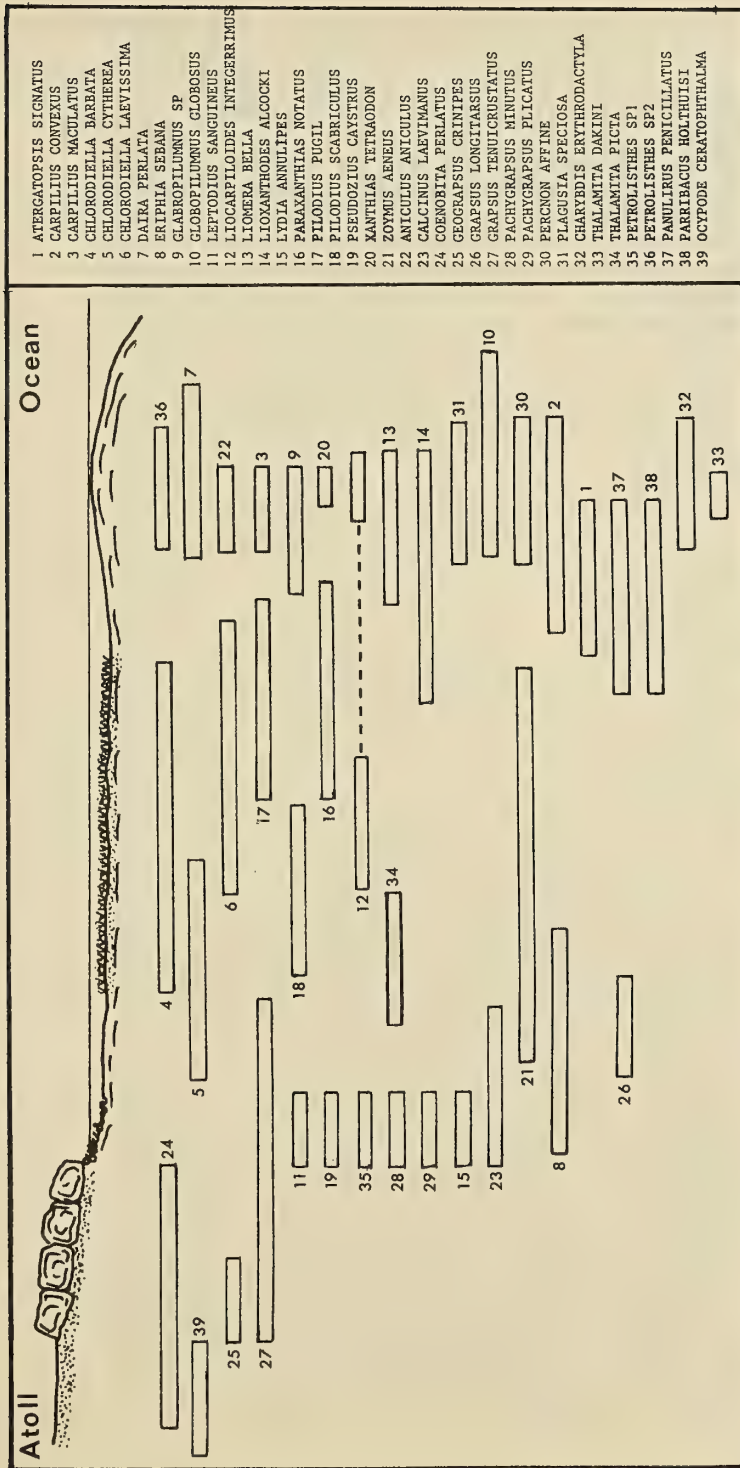


Table E : Repartition of the crustacean fauna on the sheltered outer reef.

Table F: List of fishes catalogued in Mataiva Lagoon (L) and the nearby ocean (O).

CLASS CHONDRICHTHYES**Order Carcharhiniformes****CARCHARHINIDAE**

Carcharhinus melanopterus (Quoy et Gaimard, 1824) L O

Order Rajiformes**MYLIOBATIDAE**

Aetobatis narinari (Euphrasen, 1790) L

CLASS OSTEICHTHYES**Order Anguilliformes****MURAENIDAE**

Echidna nebulosa (Ahl, 1789) L

Gymnothorax javanicus (Bleeker, 1859) L O

Gymnothorax meleagris (Shaw et Nadder, 1795) L

Order Aulopiformes**SYNODONTIDAE**

Saurida gracilis (Quoy et Gaimard, 1824) L

Order Gadiformes**OPHIDIIDAE**

Dinematichthys sp. L

Order Atheriniformes**HEMIRHAMPHIDAE**

Hyporhamphus acutus (Günther, 1871) L

BELONIDAE

Tylosurus crocodilus (Lesueur, 1821) L

Order Berycyformes**HOLOCENTRIDAE**

Myripristis kuntzei Cuvier, 1831 L

Myripristis murdjan (Forsskal, 1775) L

Myripristis sp. 417 L

Neoniphon argenteus Bleeker, 1849 L

Neoniphon opercularis Valenciennes, 1831 L

Neoniphon sammara (Forsskal, 1775) L

Sargocentron caudimaculatum (Rüppell, 1826) O

Sargocentron microstoma Günther, 1859 L

Order Syngnathiformes**FISTULARIIDAE**

Fistularia commersonii Rüppell, 1838 L

Order Scorpaeniformes**SCORPAENIDAE**

Scorpaenodes guamensis (Quoy et Gaimard, 1824) L

Order Perciformes**SERRANIDAE**

Anthias pascualus (Jordan et Tanaka, 1927) O

Anthias squamipinnis (Peters, 1855) O

Cephalopholis argus (Bloch et Schneider, 1801) L O

Cephalopholis urodelus (Bloch et Schneider, 1801) O

Epinephelus merra Bloch, 1793 L

Epinephelus microdon (Bleeker, 1856) L

Gracila albomarginata (Fowler et Bean, 1930) O

GRAMMISTIDAE

Grammistes sexlineatus Thunberg, 1792 L

PSEUDOGAMMIDAE

Pseudogramma polycantha (Bleeker, 1856) L

APOGONIDAE

Apogon exostigma (Jordan et Starcks, 1906) L

Apogon kallopterus Bleeker, 1856 L

Apogon novemfasciatus (Cuvier, 1828) L

Apogon savayensis (Günther, 1871) L

Cheilodipterus lineatus (Lacépède, 1801) L

Cheilodipterus macrodon (Lacépède, 1802) L

Cheilodipterus quinquelineatus (Cuvier, 1828) L

Fowleria aurita Valenciennes, 1831 L

Fowleria marmoratus Alleyne et MacLeay, 1876 L

Fowleria sp. 297 L

Genus sp. 289 (juv.) L

Genus sp. 292 (juv.) L

CARANGIDAE

Caranx ignobilis (Forsskål, 1775) O

Caranx melampygus (Cuvier, 1833) L O

Gnathanodon speciosus (Forsskål, 1775) L

LUTJANIDAE

Aphareus furca (Lacépède, 1802) O

Lutjanus bohar (Forsskal, 1775) O

Lutjanus fulvus (Bloch et Schneider, 1801) L O

Lutjanus gibbus (Forsskål, 1775) L O

LETHRINIDAE

Lethrinus xanthurus (Linnaeus, 1758) L

Monotaxis grandoculis (Forsskal, 1775) L O

MULLIDAE

Mulloidops flavolineatus (Lacépède, 1801) L

Mulloidops vanicolensis (Valenciennes, 1831) L

Parupeneus barberinus (Lacépède, 1802) L

Pseudupeneus bifasciatus (Lacépède, 1802) L

Pseudupeneus multifasciatus (Lacépède, 1801) L O

CHAETODONTIDAE

Chaetodon auriga Forsskål, 1775 L

Chaetodon bennetti Cuvier, 1831 L

Chaetodon citrinellus Cuvier, 1831 L

Chaetodon ephippium Cuvier, 1831 L O

Chaetodon kleinii Bloch, 1790 L

Chaetodon lineolatus Cuvier, 1831 L

Chaetodon lunula (Lacépède, 1803) L O

Chaetodon ornatissimus Cuvier, 1831 L O

Chaetodon pelewensis Kner, 1868 O

Chaetodon quadrimaculatus Gray, 1831 L O

Chaetodon reticulatus Cuvier, 1831 O

Chaetodon semeion Bleeker, 1855 L

Chaetodon trifascialis Quoy et Gaimard, 1824 L

Chaetodon trifasciatus Park, 1797 L

Chaetodon ulietensis Cuvier, 1831 L O

Chaetodon unimaculatus Bloch, 1787	L O
Chaetodon vagabundus Linné, 1758	L
Forcipiger flavissimus Jordan et MacGregor, 1898	O
Forcipiger longirostris (Broussonnet, 1782)	O
POMACANTHIDAE	
Centropyge flavissimus (Cuvier, 1831)	L O
Centropyge loriculus (Günther, 1860)	O
POMACENTRIDAE	
Abudefduf sexfasciatus (Lacépède, 1801)	L
Abudefduf sordidus (Forsskal, 1775)	L
Amphiprion clarkii (Bennett, 1830)	O
Chromis caerulea (Cuvier, 1830)	L
Chromis iomelas Jordan et Seale, 1906	O
Chromis vanderbilti (Fowler, 1941)	O
Chromis sp. 372	L
Chrysiptera leucopoma (Lesson, 1830)	L
Dascyllus aruanus (Linné, 1758)	L
Dascyllus trimaculatus (Rüppell, 1828)	O
Dascyllus reticulatus (Richardson, 1846)	O
Plectroglyphidodon dickii (Lienard, 1839)	O
Plectroglyphidodon flaviventris Allen et Randall, 1974	L
Plectroglyphidodon johnstonianus Fowler et Ball, 1924	O
Pomacentrus pavo (Bloch, 1787)	L
Pomacentrus coelestis Jordan et Starks, 1901	L
Stegastes albifasciatus (Schlegel et Müller, 1839)	L
Stegastes aureus (Fowler, 1927)	O
Stegastes nigricans (Lacépède, 1803)	L
CIRRHITIDAE	
Paracirrhites arcatus (Jordan et Evermann, 1903)	O
Paracirrhites forsteri (Schneider, 1801)	O
Paracirrhites sp. 420 (juv.)	O
SPHYRAENIDAE	
Sphyræna barracuda (Walbaum, 1792)	L
LABRIDAE	
Bodianus anthioides (Bennett, 1830)	O
Bodianus sp. 151	L
Cheilinus chlorourus (Bloch, 1791)	L
Cheilinus oxycephalus Bleeker, 1853	L
Cheilinus trilobatus Lacépède, 1801	L
Cheilinus undulatus Rüppell, 1835	L O
Cheilinus unifasciatus Streets, 1811	L
Cirrhitilabrus sp. 58	O
Coris aygula (Lacépède, 1801)	L
Coris gaimard (Quoy et Gaimard, 1824)	L O
Cymolutes sp.	L
Epibulus insidiator (Pallas, 1770)	L
Gomphosus varius Lacépède, 1801	L O
Halichoeres hortulanus Lacépède, 1801	L O
Halichoeres marginatus Rüppell, 1835	L
Halichoeres ornatissimus (Garrett, 1889)	O
Halichoeres trimaculatus (Quoy et Gaimard, 1834)	L

Halichoeres sp.(juv.)	L
Hemigymmus fasciatus (Bloch,1792)	O
Labroides dimidiatus (Valenciennes,1839)	L O
Pseudocheilinus octotaenia Jenkins,1899	L O
Pseudocheilinus tetrataenia Schultz,1946	L
Stethojulis bandanensis (Bleeker,1851)	L
Thalassoma amblycephalum Bleeker,1856	L O
Thalassoma hardwicke (Bennett,1830)	L
Thalassoma quinquevittatum (Lay et Bennett,1839)	L O
Weltmorella nigropinnata (Seale,1900)	L
Genus sp.287	L
SCARIDAE	
Hipposcarus longiceps Valenciennes,1839	L O
Scarus frenatus Lacepède,1802	L O
Scarus ghobban (Forsskål,1775)	L
Scarus gibbus Rüppell,1828	L
Scarus globiceps Valenciennes,1839	L O
Scarus oviceps Valenciennes,1840	L O
Scarus psittacus Forsskål,1775	L
Scarus rubroviolaceus (Bleeker,1849)	L
Scarus sordidus Forsskål,1775	L O
Scarus sp.(venosus)	L
Scarus sp.106 (juv.)	L
Scarus sp.107 (juv.)	L
Scarus sp.329 (juv.)	L
Scarus sp.422 (juv.)	L
BLENNIIDAE	
Enchelyurus ater (Günther,1877)	L
Istiblennius periophthalmus (Valenciennes,1836)	L
Petrocirtus xestus Jordan et Seale,1906	L
CALLIONYMIDAE	
Callionymus sp.288	L
GOBIIDAE	
Amblygobius nocturnus Smith,1956	L
Amblygobius phalaena (Cuvier,1837)	L
Asterropteryx semipunctatus Rüppell,1828	L
Callogobius sclateri (Steindachner,1880)	L
Eviota afalei Jordan et Seale,1905	L
Eviota infulata Smith,1956	L
Fusigobius neophytus (Günther,1877)	L
Gnatholepis cauerensis (Bleeker,1853)	L
Nemateleotris magnifica Fowler,1938	O
Priolepis cincta (Regan,1908)	L
Ptereleotris evides (Jordan et Hubbs,1934)	L
Ptereleotris microlepis (Bleeker,1856)	L
Vanderhorstia sp.(juv.)	L
Genus sp.290	L
Genus sp.324	L
ACANTHURIDAE	
Acanthurus glaucopareius Cuvier,1829	O
Acanthurus nigricauda Duncker et Mohr,1929	L O

Acanthurus nigroris Valenciennes, 1838	L
Acanthurus olivaceus Bloch et Schneider, 1801	L
Acanthurus pyroferus Kittlitz, 1834	O
Acanthurus triostegus (Linné, 1758)	L
Acanthurus xanthopterus Valenciennes, 1835	L
Acanthurus sp. (juv.)	L O
Ctenochaetus striatus (Quoy et Gaimard, 1824)	L O
Ctenochaetus strigosus (Bennett, 1828)	L O
Naso brevirostris (Valenciennes, 1835)	L O
Naso hexacanthus (Bleeker, 1855)	O
Naso lituratus (Bloch et Schneider, 1801)	L O
Naso unicornis (Forsskal, 1775)	L O
Zanclus cornutus (Linné, 1758)	L O
Zebrasoma rostratum (Günther, 1873)	O
Zebrasoma scopas (Cuvier, 1835)	L O
Zebrasoma veliferum (Bloch, 1795)	L O
SIGANIDAE	
Siganus argenteus (Quoy et Gaimard, 1824)	O
SCOMBRIDAE	
Katsuwonus pelamis (Linné, 1558)	O
Order Pleuronectiformes	
BOTHIDAE	
Bothus mancus (Broussonnet, 1782)	L
Order Tetraodontiformes	
BALISTIDAE	
Amanses scopas (Cuvier, 1829)	O
Balistapus undulatus (Mungo Park, 1797)	O
Balistapus viridescens (Bloch et Schneider, 1801)	L O
Melichthys niger (Bloch, 1786)	O
Melichthys vidua (Solander, 1845)	O
Pseudobalistes flavimarginatus (Rüppell, 1828)	O
Rhinecanthus aculeatus (Linné, 1758)	L
Sufflamen bursa (Bloch et Schneider, 1801)	O
OSTRACIIDAE	
Ostracion cubicus Linné, 1758	L O
TETRAODONTIDAE	
Arothron hispidus (Linné, 1758)	L
Arothron meleagris (Lacépède, 1798)	L
Canthigaster bennetti (Bleeker, 1854)	L
Canthigaster janthinoptera (Bleeker, 1855)	L
Canthigaster solandri (Richardson, 1844)	L



Reef rim sediments. Inputs by storms and high seas

Reef constructions; frame building

Bottom sediments rich in Acropora and Porites

Phosphate deposit

Carbonate basement

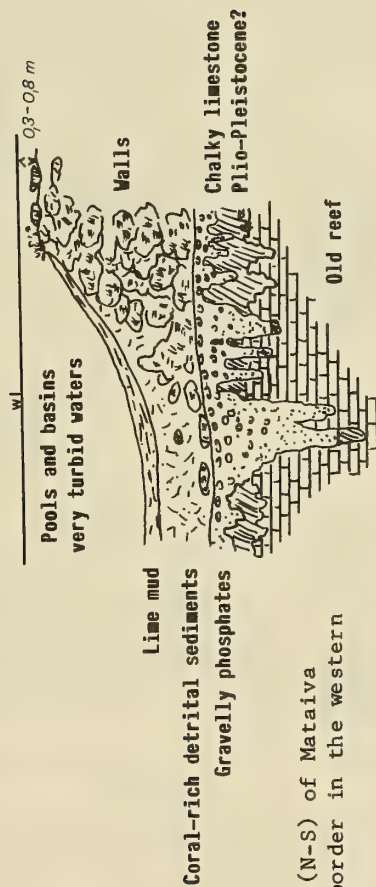


Figure 2 : Transverse cross-section (N-S) of Mataiva and detail of the basin border in the western part of the atoll.

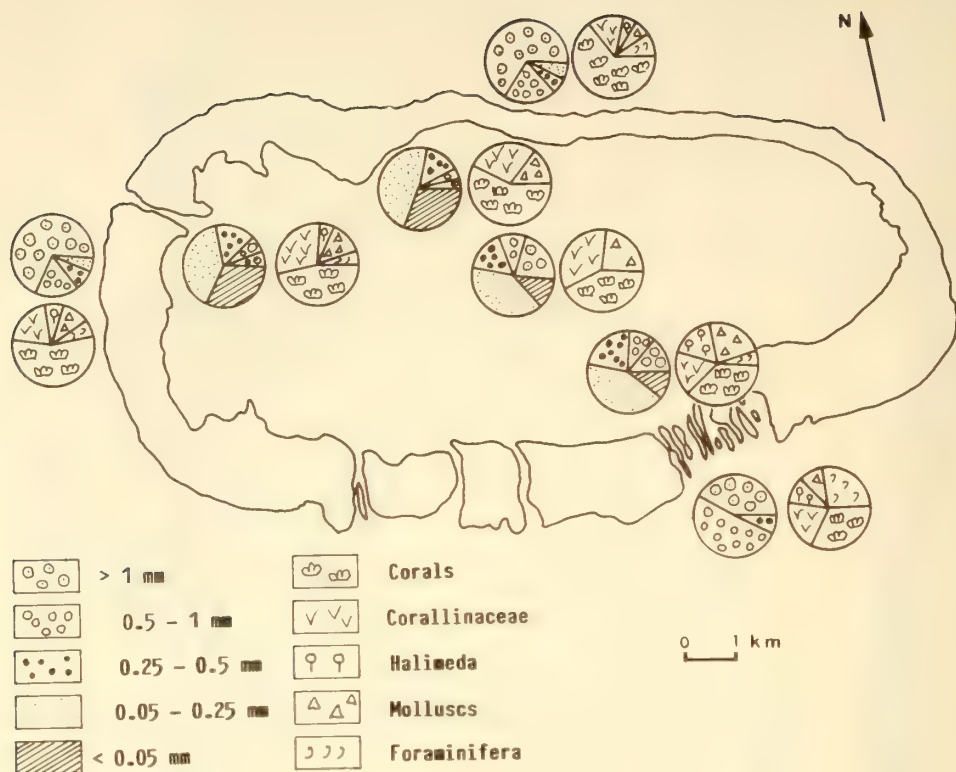


Figure 3 : Grain-size and components of lagoonal and outer reefal sediments

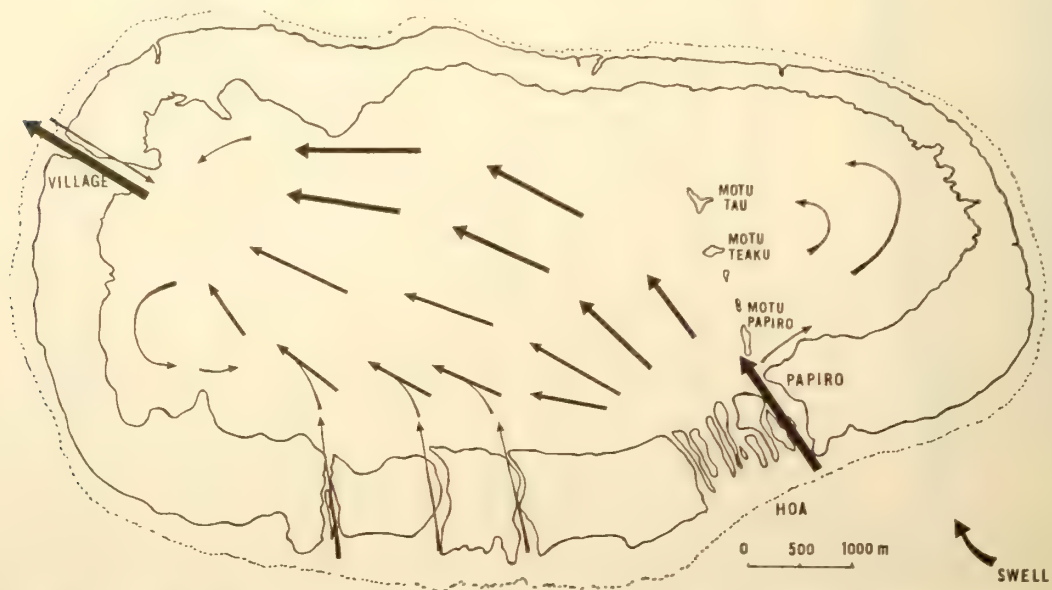


Figure 4: Surface circulation of lagoon waters (usual climatic conditions)

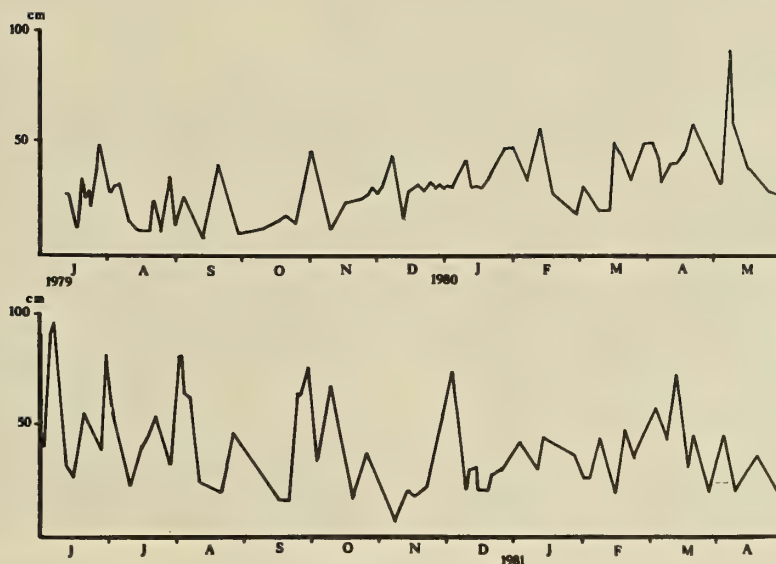


Figure 5 : Relative variations of the lagoon water level between 1979 and 1981.

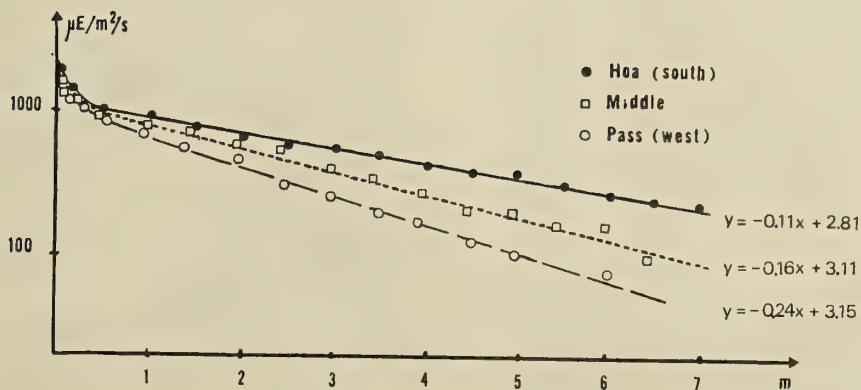
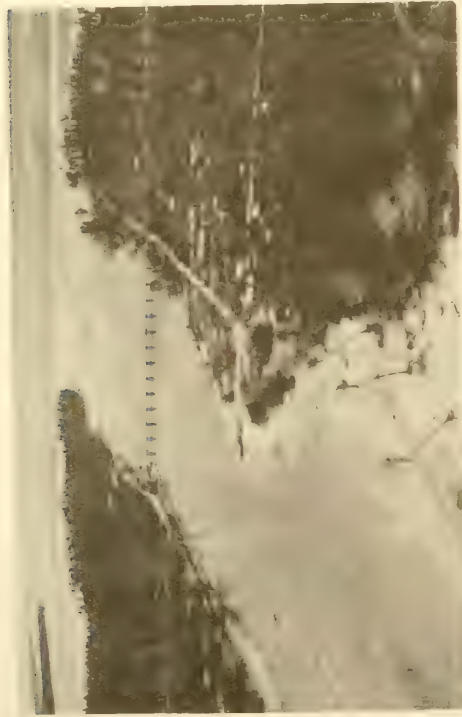


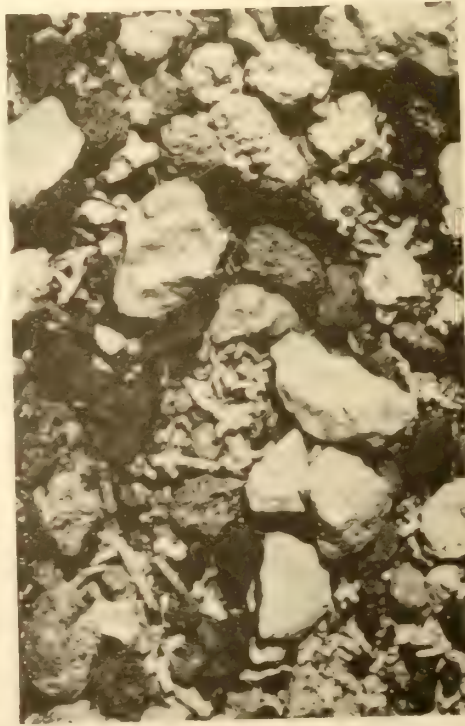
Figure 6 : Light penetration in 3 different points of the lagoon.



1. The village, damaged by the cyclone Reva in 1983



2. Aerial view of The Papiro-Aviu hoa.



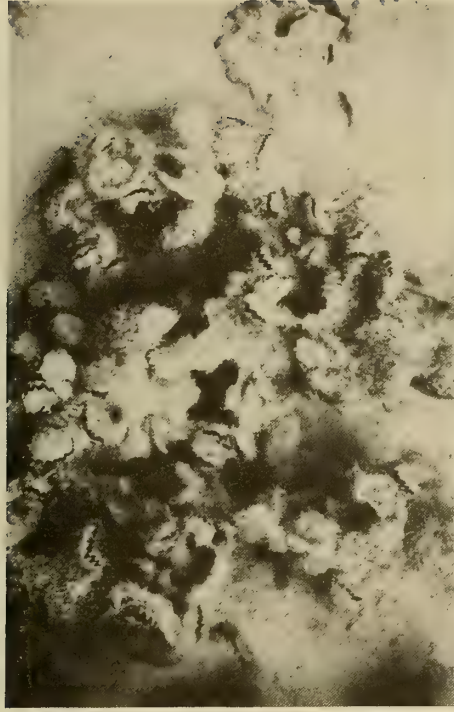
3. Dredged material including phosphates pebbles and coral fragments (Porites and Acropora).



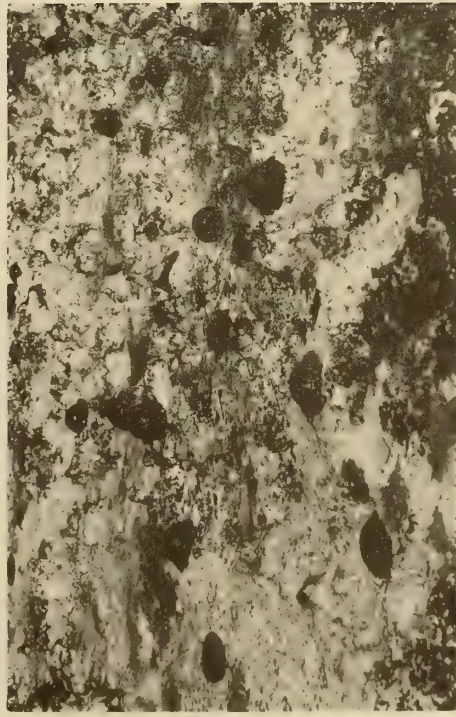
4. The flagstone of Motu Tau, with Tridacna shells in growing position.



5. Bivalves, Litophaga cinnamomina, boring Porites



6. Small oysters Crassostrea cucullata on Acropora



7. Helmet urchins, Colobocentrotus pedifer, on the southern algal ridge (Papiro).



8. The north outer slope (20 m) damaged by the hurricane Reva (Teavatia area).

ATOLL RESEARCH BULLETIN

No. 287

CHECKLIST OF THE VASCULAR PLANTS OF THE
NORTHERN LINE ISLANDS

By

LYNDON WESTER

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CHECKLIST OF THE VASCULAR PLANTS OF THE NORTHERN LINE ISLANDS

By

LYNDON WESTER *

INTRODUCTION

The Northern Line Islands consists of four atolls aligned on an axis which runs from south east to north west. The three southern islands Christmas (Kiritimati), Fanning (Tabuaeran) and Washington (Teraina) have permanent populations and are part of the Republic of Kiribati (Table 1). The fourth island, Palmyra, on the north end of the chain, is an unoccupied U.S. possession.

Table 1
Northern Line Islands

	Land area (sq. kms.)	Rainfall (millimeters)	Population	Political jurisdiction
Palmyra	0.6	4161	0	U.S.
Washington	14.2	2902	417	Kiribati
Fanning	34.6	2086	434	Kiribati
Christmas	363.4	766	1288	Kiribati

Sources: Carter, 1984; Ministry of Education, Training and Culture, 1979; Taylor, 1973.

The islands are remarkably dissimilar considering their proximity. This is in part due to the fact that they lie across an abrupt rainfall gradient. Christmas in the south, in the equatorial dry belt, receives only 766 mm of rain per year, whereas the islands further north are influenced by the intertropical convergence to a progressively

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greater extent. Palmyra, four degrees of latitude north, receives 4161 millimeters per year and supports a luxuriant forest.

The islands are also quite different in form. Christmas is a very large atoll; most of the land is one continuous surface which almost completely encircles an embayment or lagoon and there is a large protruding peninsula off to the southeast. The island contains extensive plains of limestone hardpan, numerous shallow pools, beach berms and sand dunes. The ocean coast is characteristically a sandy beach. Fanning on the other hand corresponds more closely to the popular image of an atoll as it is made up of three long, narrow islands which surround a shallow lagoon. Its ocean shore is covered almost completely with plate-like coral shingle and little sand. Washington is perhaps the most peculiar island of the group. It has the smallest coral platform and the island is lens-shaped. Instead of a lagoon open to the sea the central depression of the island contains a freshwater lake and two peat bogs. The shore has a narrow fringing reef usually covered on the landward side with a thin strip of sand. Although Palmyra is a slightly larger coral structure than Washington, it is mostly submerged reef. At the time of first survey the atoll consisted of about fifty tiny islets heavily vegetated down to high tide level; however dredging and reclamation have greatly increased its area.

The islands were uninhabited at the time of European discovery but there is ample evidence of former Polynesian occupancy (Emory, 1934, 1939; Finney, 1958). Whalers and traders stopped at the islands during the early nineteenth century but the first attempt at settlement was by a group from Hawaii in 1820. The colony of about forty people included both Europeans and Hawaiians but appears to have been a failure because most of the party had returned by 1822 (Maria Loomis, 1819-24; Elisha and Maria Loomis, 1820-24). Whalers who stopped by the island for wood or coconuts recorded an occasional castaway over the next two decades. However by 1840 a white man and 30 Society Islanders were living on the island and able to supply one of the ships engaged in the U.S. Exploring Expedition with "watermelon, taro and pumpkins" (Anonymous, 1838-41). Two years later a whaler reported the group was engaged in producing coconut oil and supplied them with arrowroot (Hussey, 1841-45). Edward Lucett arrived on Fanning in 1846 with a title and the intention of establishing a coconut oil industry. He noted that there was a "man of Crusoe habits" on the island who had an Hawaiian wife and a large family of children and grandchildren and was engaged in the raising of pigs. What happened to the earlier colony or whether this represented a relict of it is not clear (Lucett, 1851). In 1852 John English purchased the establishment and by 1854 seems to have expanded to Washington Island because a whaler who stopped there reported he was able to trade for "sweet potatoes, coconuts and bananas" (English, 1857; Holley, 1853-57). Washington has no safe anchorage and it may have been occupied only intermittently because when another whaler stopped there in 1861 he noted that the natives could provide nothing because they had only been there for a few months (Greene, 1860-65). English sold his interests in the islands to William Greig, his assistant, and George Bicknell in 1864 who switched to the

production of copra and were responsible for extensive planting of coconut on both Washington and Fanning. When George Bicknell died the operation of the plantation passed to the Greig family who remained there well into the twentieth century.

Drought-prone Christmas Island with only small natural stands of coconut had little to offer whalers except turtles and fish. Phosphate attracted guano diggers to Christmas Island in 1858 and some rock was also exported from Fanning Island between 1878 and 1881 but the Northern Line Islands were not among the major producers of phosphate rock. It was not until 1882 that more or less permanent occupation began on Christmas. Messrs Macfarlane and Henderson of Auckland took possession of the island in the name of their company and over the next few years their employees were engaged in the gathering of pearl shell from the lagoon and the planting of coconuts (Bailey, 1977).

When the British Commonwealth communications cable was constructed across the Pacific from Canada to Australia, a relay station was built on Fanning Island which operated from 1902 to 1963. This imposing facility, which had a permanent staff and could boast of a swimming pool, tennis courts and extensive gardens, enhanced the position of Fanning as the focus of human activity in the Line Islands. In 1902 Lever Brothers Ltd. acquired a lease of Christmas Island and financed a major coconut planting program. The Greigs and the heir of James Bicknell were forced to sell their interests in Washington and Fanning Island in 1907 although members of the Greig family remained to manage the plantation. The purchaser was Emmanuel Rougier who conveyed them to a company called Fanning Island Limited just a few years later. Meanwhile by 1914 he had taken over the Lever lease of Christmas Island and formed the Central Pacific Coconut Plantations Limited. He and later his nephew Paul Rougier ran the islands as a plantation. The Gilbert and Ellice Islands Company took over the running of the Christmas Island coconut plantation in 1941 after Paul Rougier became embroiled in criminal and political affairs and returned to France (Bailey, 1977). Washington and Fanning, the wetter and more productive islands, were acquired by Burns Philp & Co. who continued to operate them as coconut plantations until they sold them to the Kiribati government in 1983 (Republic of Kiribati, 1983).

During the Second World War New Zealand and American troops were garrisoned on Christmas Island and in 1956-58 Britain used the island for nuclear testing. The United States used it for similar purposes in 1962. All devices were detonated in the atmosphere and its most conspicuous martial legacy is 100 kilometers of sealed road and impressive quantities of abandoned equipment and rusting structures.

Palmyra Island escaped permanent settlement or significant modification until the United States established a military base there in 1940 which was eventually expanded to accommodate 6,000 personnel. The transformation of the island by dredging the lagoon, constructing causeways and building airstrips has been described in detail by Dawson (1959). The island was abandoned as a base in 1958 and plans to develop it as a plantation or a resort have come to nothing. It remains an

uninhabited U.S. possession recovering from profound disturbance.

In 1979 the Gilbert, Phoenix and Line Islands, formerly administered by the British, became Kiribati, an independent republic. It is the hope of the government to use the Line Islands, particularly Christmas, to settle people from heavily overpopulated South Tarawa, in the Gilbert group. However the economic prospects for development of the Line Islands are small, and the problem of transport and communication with the administrative and population center far to the west, is great. Improvements to the airport and the construction of an hotel were sponsored by the Japanese government who built and maintains a down-range missile tracking station on Christmas Island. A small tourist industry exists on Christmas based on game fishing and some fish are exported to Honolulu. Copra production has diminished almost to zero. However the government is presently engaged in a study of the agricultural potential of the newly acquired Washington and Fanning Islands.

SUMMARY OF THE LAND FLORA

The indigenous land flora of vascular plants consists largely of widespread strand and coral island species. Endemism is low, as is to be expected on an atoll. The only endemic species which have been described from the islands belong to genera which, for one reason or another, pose many problems for the systematist. Hence the status of these taxa (Asplenium pacificum, Pandanus fanningensis, P. hermsianus, four varieties of P. fischerianus, Portulaca fosbergii and P. johnii) is in doubt. Only nine indigenous species, out of a total of 42, occur on all of the islands in the group and the significant differences in the floras, and the character of the vegetation communities, can be related to rainfall (Table 2). The smaller but wetter islands (Palmyra and Washington) are mostly covered by closed forest and have more indigenous species than the much larger Christmas Island. The vegetation of the latter consists of either sickly coconut plantation or low scrub. Fanning receives sufficient rainfall to support closed canopy forests of Cocos, Pisonia and Pandanus but extensive tracts of land are inundated during high tides and these mudflats support mainly Lepturus grass.

Table 2
Origin and status of species

	Indigenous	Cultivated or persisting	Adventive	TOTAL
Palmyra	21	14	23	58
Washington	25	46	20	91
Fanning	23	70	30	123
Christmas	19	25	25	69

Similarity indices calculated on the basis of the entire indigenous flora (Table 3) show a high level of similarity between Palmyra and Washington and, to a slightly lesser extent, between those two islands and Fanning. Christmas, on the other hand, is quite dissimilar from Palmyra and Washington but bears considerable similarity to Fanning.

Table 3
Similarity indices: indigenous species

	Washington	Fanning	Christmas
Palmyra	78.2	63.6	40.0
Washington		62.5	36.4
Fanning			61.9

Calculations based on Sorensen index of similarity

$$SI = \frac{\text{number of species common to both islands}}{1/2 (\text{total species on island A} + \text{total species on island B})} \times 100$$

The concentration of introduced species shows a distinctly different pattern. Fanning has many more cultivated and adventive species, which can probably be explained by its suitability for horticulture and its long history as the headquarters for the main plantation on the islands. Kyte (1861) remarked on the variety of crops which were grown on the plantation and the owners went so far as to bring soil from Honolulu for their gardens. Many other plants were imported for the extensive gardens of the Cable Station and even today a number of ornamental species persist despite the lack of care. Washington might have been equally suitable to support crops plants or ornamentals but it lacks a safe anchorage and so fewer introductions have occurred. Most of the exotic species recorded from Palmyra were introduced when it served as a military base. The severely disturbed areas are still suitable habitats for adventive species but the introduced plants will probably be replaced if no further human interference occurs. It would appear that some adventive species recorded in the nineteenth century have since disappeared. The guano digger John Arundel for example collected Achyranthes aspera and Asclepias curassavica on Fanning but they have not been recorded since and we can assume they are locally extinct.

There is a much lower level of similarity between the assemblages of adventive species on the different islands (Table 4). Furthermore the patterns of similarity are somewhat different. The highest similarity is between Fanning and Washington which is probably because they are both wet, have experienced similar human use and indeed been operated as a single plantation for most of their recent history.

Table 4
Similarity indices: adventive species

	Washington	Fanning	Christmas
Palmyra	41.9	45.3	45.8
Washington		56.0	53.3
Fanning			43.6

The pattern of similarity between the cultivated species on islands shows a similar pattern to that of the adventives (Table 5). Fanning and Washington again show a high level of similarity furthermore Fanning, Washington and Christmas together as a group seem to have much in common but are quite dissimilar from Palmyra. This may be because Palmyra has had a very different history of human occupation and disturbance.

Table 5
Similarity indices: cultivated or persisting

	Washington	Fanning	Christmas
Palmyra	30.0	21.4	35.9
Washington		65.5	53.5
Fanning			46.3

PLANT COLLECTORS OF THE NORTHERN LINE ISLANDS

Of the four islands of the Northern Line Islands, Christmas and Fanning have received most attention from plant collectors because they are more accessible. A few specimens remain from collections gathered in the nineteenth century but the first systematic inventories were made by participants in expeditions sent by the Bishop Museum in the 1920's and 30's. Since that time there have been other efforts which have added one or two new indigenous species to the known flora and made it possible to keep track of introductions. A summary of information about each of the collectors who have worked in the Northern Line Islands, and the disposition of their specimens, has been compiled for reference.

Arundel, John T. was a trader and guano digger who became one of the leading figures in the Pacific phosphate industry (Langdon, 1974). He was at first a field manager for the British firm of Houlder Bros. and Co. which operated in the equatorial Pacific islands. He later went into the business himself and, between 1883 and 1891, operated from Apia using mostly Niue and Cook Island laborers. At various times he held leases for many of the dry guano islands. He traveled extensively and is known to have visited the Line Islands in 1873. Between 1879 and 1881 he directed the guano mining on Fanning (Arundel, 1870-1919). On

one these trips he apparently collected 21 specimens on Fanning and other islands, which were sent to Joseph Hooker at Kew (Arundel, 1890). From these a list was compiled (Anonymous, 1874-86) which was reported in part by Hemsley (1855) in the results of the Challenger Expedition. His specimens are preserved at Kew.

Ball, Stanley C. was a zoologist and Curator of Collections at the Bishop Museum who participated in the Fanning Island Expedition in the company of C.E. Edmondson. They made comprehensive biological collections during a ten day stay on Fanning in July and August 1922 (Edmondson, 1923; Gregory, 1923). Ball made the collections of plants which, along with his field notebooks, are in the Bishop Museum. In 1924 Ball was on Christmas and again on Fanning Island but this time in the company of G.P. Wilder as members of the scientific party on the "Cruise of the Kaimiloa" sponsored, in part, by the Bishop Museum. Ball made no further collections at this time.

Bennett, Frederick Debell was the surgeon on board a whaling ship which circumnavigated the globe between 1833 and 1836. During the voyage he stopped on Christmas Island (6-10 May, 1835) and made extensive plant collections. A list of the plants collected was published along with his account of the voyage (Bennett, 1970). His specimens from this voyage were sent to Berlin Herbarium (Lanjouw and Staflen, 1954) and presumably destroyed during the Second World War. It is possible that some duplicates may exist at the British Museum or at Kew.

Bergman, H.F. and Erling Christophersen were botanists on the Whippoorwill Expedition sent to the Line Islands by the Bishop Museum. Bergman was responsible for systematic collecting and made extensive collections while on Christmas (31 July and 7 August) and on Washington (13-18 August 1924) (Gregory 1925). He also visited Fanning with other members of the expedition but on this island Christophersen seems to have made all of the collections. His specimens are preserved in the Bishop Museum and the U.S. National Herbarium and were used in the preparation of a detailed report on the vegetation of the islands by Christophersen (1927).

Browne, Ashley was employed by the University of Hawaii Agricultural Extension, and selected as a member of the official party of a ship dispatched to supply a group of young men from Honolulu who were living on the Southern Line Islands (Bryan, 1974). The ship stopped at Palmyra on 17 October 1939 during which time Browne collected a few specimens which are now at Berkeley.

Bryan, Edwin H. was Curator of Collections at the Bishop Museum when he made at least two stops on Palmyra Island during the 1930's. He travelled with ships which transported and supplied young men from Honolulu who were sent to occupy the Southern Line Islands in an effort to strengthen the United States's claim to that territory. In the course of these voyages the ships visited the Northern Line Islands. During stops on Palmyra (23 March 1935 and 11-12 August 1938) Bryan took the opportunity to make collections of plants (Bryan, 1974). His specimens

are in the Bishop Museum and the U.S. National. However the labels show confusion, in some cases, about the site of collection.

Christophersen, Erling and H.F. Bergman were the botanists on the Whippoorwill Expedition sent by the Bishop Museum to survey the Line Islands. It was the responsibility of Christophersen to study the ecological aspects of the islands. However he also made all the collections on Fanning during their stay (29-30 July) and both men collected while they were on Christmas (31 July to 7 August) (Gregory, 1925). However all the collecting on Washington appears to have been done by Bergman. Christophersen wrote a detailed report of the vegetation of the Line Islands based on these observations (Christophersen (1927).

Cooke, Charles Montague Jr. was a malacologist at the Bishop Museum who accompanied Henry Cooper and Joseph Rock on an expedition to Palmyra Island in 1913 (Rock 1916). He was a leader of "Trip B" of the Whippoorwill Expedition which visited the Line Islands again in 1924 (Gregory, 1924); however all of their important work was done on Baker and Howland Islands. Cooke was the leader of the Mangarevan Expedition, sponsored by the Bishop Museum, which stopped at Fanning Island (20-29 April 1934) on the way south. In the course of the return journey they called at Christmas Island (21-22 October) and again at Fanning (23 October). The botanists of the party were Harold St. John and F. Raymond Fosberg who did most of the collecting independently of Cooke (Kondo and Glench, 1952).

Cooper, Henry E. was a judge in Honolulu and President of the Board of Regents of the College of Hawaii. In 1913, soon after purchasing the island of Palmyra, he took a group of scientists on an expedition of exploration. Joseph Rock wrote the report of the trip (Rock, 1916). Cooper was listed along with C.M. Cooke as a collector on that expedition. However Cooper collected plants independently on another visit to Palmyra in 1914. All specimens were given to the Bishop Museum.

Dawson, E. Yale, a marine biologist, was on Palmyra (15-21 October 1958) for the purpose of studying ciguatera fish poisoning. He documented the considerable changes caused by the construction of a military base on the island during the Second World War (Dawson, 1959). His extensive collections of both native ruderal and cultivated species are preserved in the Bishop Museum and the U.S. National Herbarium.

Fosberg, F. Raymond first visited the islands as a member of the Mangarevan Expedition which stopped at Fanning Island (20-29 April 1934) during the journey south and at Christmas Island (21-22 October) and again at Fanning (23 October) on the voyage home. At this time Fosberg was acting as an assistant to Harold St. John. Fosberg again collected on Christmas Island (16 August 1936) in the company of Alfred Metraux and his wife E.M. Metraux. His specimens are in the Bishop Museum and the U.S. National Herbarium.

Gallagher, M.D. was a major in the British armed forces stationed on Christmas Island from June 1958 to mid June 1959 during a series of atomic tests. He was the founder and guiding spirit of the Natural History Society of Christmas Island established for the purpose of fostering interest in wildlife. A series of bulletins were issued which contained useful information about the plants and animals of the island (Anonymous, 1962). Major Gallagher made collections of plants which he sent to the Bishop Museum and published an article based on his observations of the birds (Gallagher, 1960).

Hamilton, Dean C. made collections and observations of plants on the northern portion of Christmas Island in the vicinity of Main Camp while conducting an entomological survey of the island for the Plant Quarantine Division, Agricultural Research Service of the United States Department of Agriculture (11-14 April 1962). In collaboration with Alvin K. Chock, then of the Botany Department, Bishop Museum, a list of plants of the island was published in the Atoll Research Bulletin (Chock and Hamilton, 1962). The specimens are preserved in the Bishop Museum.

Herms, William B. was an entomologist from the College of Agriculture of the University of California, Berkeley who, with Harold Kirby Jr., a graduate assistant, spent four months in the Line Islands investigating the pests of coconut. He spent most of his stay from 3 May to 27 July 1924 on Fanning Island. However he and his assistant made a short foray to Washington Island (13-16 May) during which Herms was largely incapacitated (Herms, 1925; 1926). They made collections of plants on both islands. Christophersen (1927) informs us that E.D. Merrill prepared a manuscript of a flora of the islands based on these collections and that it was preserved in the Bishop Museum library. A search was made for this manuscript but it could not be located. However Christophersen further stated that he had incorporated its information into his published work.

Hill, F.L. made collections on Christmas Island on 25 October 1957 and they are presently in the Bishop Museum. No other information about the collector has been found.

Hill, Margaret was a school teacher employed by the Civil Aeronautics Authority during the time they maintained a base on Palmyra Island. In October 1949 she made a collection of 25 plants from the vicinity of the inhabited area of Menge islet. The plants, mostly ruderals, were identified by Marie C. Neal and E.H. Bryan and are preserved in the Bishop Museum (Dawson, 1959).

Jenkin, R. N. and M.A. Foale conducted a study of the potential of Christmas Island for growing coconuts for the Directorate of Overseas Studies of the British Government during 1965 and 1966 (Jenkin and Foale, 1968). They spent August and September 1965 on Christmas Island doing the field portion of the study and during that time Jenkin collected plant specimens. At least some of the specimens are at Kew.

Judd, Albert F. was a trustee of the Bishop Museum who went as a member of the official party on the ship supplying groups of young men sent to

occupy the Southern Line Islands. He and D. Mitchell made collections while on Palmyra Island (13 June 1935) which were placed in the Bishop Museum.

Kirby, Harold Jr. was a graduate student in zoology from the University of California who accompanied William Herms to Fanning, and presumably Washington Island, to study insect pests attacking the coconut. Extensive collections on both islands were made. They arrived at Fanning on 3 May and Kirby remained until 3 October although Herms left near the end of July. They made a short foray to Washington (13-16 May) (Herms, 1925; 1926). Otherwise most of Kirby's time was spent on Fanning although he joined the scientific party of the Whippoorwill Expedition sent by the Bishop Museum when they stopped on Fanning (Gregory, 1925).

Lee, Mary Ann Bacon, a geographer from the University of Iowa, spent several weeks on Fanning in July 1983 to conduct a study of the effect of land crabs on the germination and spread of seeds. She collected plants mainly in the vicinity of the Cable Station and they are preserved in the Bishop Museum.

Long, C.R. participated in the Pacific Ocean Biological Survey whose goals included an inventory of the terrestrial flora of islands of the Northwest Hawaiian Chain and the atolls of the Central Pacific. Long made two voyages to the Line Islands, during which he collected extensively. In the course of the first trip in 1964 he stopped on Palmyra (6-7 June), Washington (9-10 June) and Christmas (14-16 June) on the way south and at the same islands on the return trip Christmas (21-23 November), Washington (25-26 November), and Palmyra (27-28 November). In the following year on the return leg of a voyage to the southern islands he stopped again on Christmas Island (25-30 June) and for the first time on Fanning (2 July). The main set of his specimens, his collection records and notebook are housed in the herbarium of the Bishop Museum. There are in additional specimens in the U.S. National Herbarium.

Metraux, Alfred, an anthropologist and ethnologist, along with his wife E.M. Metraux, was on Christmas Island (16 August 1936) with Fosberg and made extensive collections which are now in the Bishop Museum and U.S. National Herbarium.

Mitchell, Donald D., of Kamehameha Schools in Honolulu, travelled with the official party on the ship taking former students from the school who were sent to occupy the Southern Line Islands. He was on Palmyra Island (13 June 1935) and, in the company of A.F. Judd, made collections of plants which are preserved in the Bishop Museum (Bryan 1974).

Moeller, Henry S. collected on Palmyra Island (28 December 1959 to 3 January 1960) and his specimens are preserved in the Bishop Museum.

Perry, Roger collected on Christmas (August 1979) and on Washington (June 1979) islands. His specimens are in Kew.

Rock, Joseph Francis Charles was a botanist at the College of Hawaii (which was later to become the University of Hawaii) who made important

contributions to the understanding of the flora of Hawaii and China. He and a zoologist from the Bishop Museum were invited by the owner of Palmyra, Henry E. Cooper, to accompany him on an expedition to that island in 1913. They made extensive collections between July 12 and 28th and Rock wrote a detailed description of the island illustrated by excellent photographs (Rock, 1916). The publication, produced in cooperation with several specialists, includes lists of fungi, lichens, mosses, ferns and higher plants as well as descriptions of new species and forms. Specimens are preserved in the Bishop Museum and the U.S. National Herbarium. Rock also wrote a popular account of the trip which was published in the Atlantic Monthly (Rock, 1929).

Russell, Dennis J. and Roy T. Tsuda collected on Fanning Island in July 1972 while they were graduate students in botany at the University of Hawaii. Their specimens were presented to the Bishop Museum and were consulted by Harold St. John when he prepared the flora of Fanning (St. John, 1974).

St. John, Harold was the botanist on the Mangarevan Expedition led by C. Montague Cooke and sponsored by the Bishop Museum. With the assistance of F. Raymond Fosberg he collected on Fanning Island (20-29 April 1934) during the southward passage and on Christmas Island (21-22 October) and Fanning (23 October) on the voyage back to Honolulu (Gregory, 1935). Collections were made by St. John and Fosberg as well as St. John and Cooke. The specimens are preserved in the Bishop Museum. St. John also made the determinations of the specimens collected by Russell and Tsuda on Fanning in 1972 and prepared a flora of this island (St. John, 1974).

Tsuda, Roy T. and Dennis J. Russell collected on Fanning in July 1972 while they were graduate students in botany at the University of Hawaii. Their specimens were presented to the Bishop Museum and were consulted by Harold St. John in the preparation of the flora of the island (St. John, 1974).

Streets, Thomas H. was the assistant surgeon on board the U.S.S. Portsmouth, commanded by Joseph S. Skerrett, which was engaged in the United States North Pacific Surveying Expedition between 1873 and 1875. This was a hydrographic survey conducted by the U.S. Navy to check hazards to navigation in the Pacific and Lower California. In the course of this they stopped on Palmyra (12-27 December 1873), Washington (31 December 1873 to 3 January 1874), Fanning (4 January 1874) and Christmas Islands (14-22 January 1874) (Skerrett, 1873-4). Streets and the surgeon, William H. Jones, made plant collections and gathered information on animal life sufficient to write three articles on the birds and natural history of the islands (Streets, 1876, 1877a, 1877b). Most of the plant specimens were sent ahead to Asa Gray who made determinations. By the time Streets returned from the expedition the specimens had been distributed through the herbarium of the Department of Agriculture. No complete list of the specimens had been made. The list later published by Streets was based on duplicates he had retained of material collected on Palmyra, Washington and Christmas Islands (Streets, 1877a). Some of Streets' specimens are in the U.S. National Herbarium. On the labels the

collector was first shown as Dall (or Dale) but this has been crossed out and replaced by the name Dr. Streets.

Wester, Lyndon L. made collections during two trips to the Northern Line Islands. In the course of a reconnaissance of the vegetation in 1982 he collected on Fanning (4-11 August), Washington (6 August) and Christmas (12-19 August). In the following year a longer stay was made on Washington Island (7-21 August) in the company of James O. Juvik and Paul Holthus for the purposes of conducting a vegetation survey and obtaining peat from the bog for pollen analysis. Transport to Washington required stops on Fanning Island and some additional collecting was done (6-7 and 21-22 August). All specimens are preserved in the Bishop Museum.

Wilder, Gerrit Pamile was an horticulturalist who, along with S. Ball, was a member of the scientific party on the "Cruise of the Kaimiloa". Wilder made plant collections during stops on Fanning (27 November to 7 December 1923) and Christmas (8-17 December). The specimens were deposited in the Bishop Museum (Gregory, 1925).

CHECKLIST

In the list of species below the presence of a species on one or other of the Northern Line Islands is indicated by the symbols P (Palmyra), W (Washington), F (Fanning) or C (Christmas). This is followed by the names (abbreviated) of the person, or persons, who have collected specimens consulted for this work. In some instances parties of two or three collectors visited an island at the same time and made collections both individually and in pairs or trios. The various combinations of collectors were not differentiated and any plants collected by members of that group are designated in the same manner. The abbreviations for collectors and groups of collectors are indicated below.

Most of the specimens taken from the Line Islands are in the herbarium of the Bernice P. Bishop Museum, Honolulu. The location of a specimen is indicated in round brackets () after the collector's name only if it is housed in an herbarium other than the Bishop Museum.

A few important specimens seem to be lost, or at least not found in the obvious place for them. They are shown in square brackets []. Species not represented by specimens in herbaria at all, but which have been directly observed by the author or recorded in the literature by a reliable source, are designated "observed".

Adl	Arundel	HiF	Hill, F.L.
Bal	Ball	HiM	Hill, Margaret
Ben	Bennett	Jen	Jenkin
Ber	Bergman	J&M	Judd and Mitchell
Brn	Brown	Lee	Lee
Bry	Bryan	Lng	Long
Cht	Christophersen	Moe	Moeller
Cok	Cooke	Pry	Perry
Cop	Cooper	RCC	Rock, Cooke and Cooper
Cur	Curlett	R&T	Russell and Tsuda
Daw	Dawson	StJ	St. John
F&M	Fosberg and Metraux	S&F	St. John and Fosberg
Gal	Gallagher	SFC	St. John, Fosberg and Cooke
Gri	Griggs	Sdg	Sledge
Ham	Hamilton	Str	Streets
H&K	Herms and Kirby	Wes	Wester
		Wil	Wilder

* Introduced by Polynesians or in historic time

[] Specimen was not seen.

() Herbarium where the specimen is housed if other than Bishop Museum.

Herbaria

K Kew
 UC University of California, Berkeley
 US U.S. National Museum of Natural History.

PSILOACEAE

Psilotum nudum (L.) Beauv.

Found mostly as an epiphyte on bases of coconut trunks.

P - Daw, Lng(K)

W - Ber, Pry(K), Wes

F - R&T, Wes.

ASPLENIACEAE

Asplenium nidus L.

Holtum described A. pacificum from a plant grown at Kew. The spores were obtained from a specimen collected on Washington Island. However the status of this taxon, as distinct from A. nidus, will only be clear when the genus is studied more closely. It is one of the most common epiphytes and understory species on Palmyra and Washington.

P - RCC, Bry(K), Bry

W - Ber, H&K(UC), Sdg(K), Pry(K), Wes.

NEPHROLEPIDACEAE

Nephrolepis exaltata Schott

Locally abundant as an epiphyte on trunks in understory. Some doubt exists about this species. Sledge did not give a specific name to the specimen he collected and F. M. Jarrett felt that the Perry specimen was intermediate between E. biserrata and E. hirsutula.

W - Str(US), Ber, Pry(K), Wes.

N. hirsutula Forst.

Appears on Palmyra and shows distinct differences from the species on Washington..

P - Daw, Lng.

POLYPODIACEAE

Phymatodes scolopendria (Burm. f.) Ching

Very common epiphyte and forms dense understory in coconut forest.

Recorded as Polypodium aureum by Streets and Polypodium scolopendria or Microsorium scolopendria several others.

P - RCC, J&M, Brn.

W - Str(US), Ber(K), H&K(UC), Wes.

F - Adl(K), Bal, Cht, H&K(UC), R&T, Wes.

ARAUCARIACEAE

*Araucaria sp.

A few large trees planted as ornamentals around the Cable Station on Fanning.

F - R&T, Wes.

1.

PANDANACEAE

Pandanus sp.

A new species recognised by St. John but not yet published.

F - STC.

1. Fosberg (Kew Bull. 31:837-840, 1977) regards all of the Pandanus taxa listed here as minor taxa, cultivars, or individuals of Pandanus tectorius Parkinson.

P. fanningensis St. John

A species known from only two specimens collected in 1972 near the Cable Station on Fanning.

F - R&T.

P. fischerianus Martellivar. rockii (Mart.) B.C. Stone

A specimen from Palmyra collected by Rock was described by Martelli (in Rock 1916) as a new species, P. rockii. However Stone (1968) believed this taxon is better regarded as a variety of P. fischerianus.

P - RCC, J&M, Moe.

var. cooperi (Mart ex Rock) B.C. Stone

Material collected by Rock from Palmyra was described by Martelli (in Rock, 1916) as a new variety of P. pulposus (var. cooperi Mart. ex Rock). However after intensive study of the Pandanus of the Marshall Islands Stone (1968) concluded that this taxon is better regarded as a form of P. fischerianus.

P - RCC

*var. pulposus (Warburg) B.C. Stone forma bergmanii (F.Br.) B.C. Stone

A specimen collected by Bergman on Washington Island was described by Brown (1930) as a new species, P. bergmanii F. Br.. Stone (1968) believed this to be a cultivated variety similar to some found in the Gilbert Islands and possibly introduced by workers. He concluded that this taxon should be regarded as a form of P. fischerianus.

W - Ber

var. bryanii B.C. Stone

A specimen collected by Bryan on Palmyra in 1935 was described as a new variety of P. fischerianus by Stone (1968). St. John (1983, pers. comm.) believes that this taxa should be raised to the species level but he has not published the new name. This wild species has also been collected on Washington Island.

P - Bry.

W - Wes.

P. hermsianus Mart.

A single phalange collected on Fanning Island by Herms was the basis upon which Martelli (1926) described the species P. hermsianus Mart. He believed the phalange had drifted from elsewhere and that the species was not native to Fanning. Stone (1968) thought there was insufficient material to create a new species but St. John (1972) concluded that a specimen he and Fosberg collected on Fanning in 1934 belonged to this taxon and was able to provide a more complete description.

F - H&K(UC), S&F.

*P. tectorius Parkinsonvar. nova-caledonicus Mart.

St. John (1972) believes this to be a cultivated species introduced to Fanning Island by Gilbertese laborers. Furthermore he thinks the specimen collected by Long in 1965 is the same as one photographed by Herms in 1924.

F - Lng

POTAMOGETONACEAE

Potamogeton sp.

A sterile specimen, said to have been collected by Bergman in the lake of Washington Island (Christophersen, 1927).

W - [Ber].

POACEAE

*Cenchrus echinatus L.

A common grass on atolls but perhaps not native.

P - HiM.

W - Wes.

F - S&F, R&T, Wes.

C - Gal, Ham, Wes.

*Chloris inflata Link

An adventive on Palmyra in 1949 (Dawson, 1959).

P - HiM

*Cynodon dactylon (L.) Pers.

A common lawn species on Washington and Fanning.

W - Ber, Wes.

F - H&K(UC), Wes.

*Dactyloctenium aegyptium (L.) Willd.

An uncommon weed in waste areas around Napia village on Fanning.

Perhaps a new arrival.

F - Wes.

Digitaria pacifica Stapf

This is the Syntherisma pelagica F. Brown (variety b) which was described in Brown (1931) and the plant identified by Christophersen (1927) as Panicum stenotaphrodes Nees. ex Stend.

C - Ber, SFC, F&M, Gal, Lng, Wes.

*Digitaria sp.

In grassy areas around village on Washington. Said by one of the residents to be a new arrival.

W - Wes.

*Eleusine indica (L.) Gaertn.

A common volunteer in waste places.

P - Daw.

W - Ber, Wes.

F - S&F, R&T, Wes.

C - Gal, Ham, Lng, Wes.

*Eragrostis ciliaris (L.) R.Br.

Rare in waste areas.

C - Wes.

*E. pilosa (L.) Beauv.

Rare in waste areas

C - Wes.

*E. tenella (L.) Beauv. ex R. & S.

Recorded as E. amabilis (L.) Wight and Arnott by Christophersen (1927) and Chock & Hamilton (1962). A common weed.

W - Ber, Wes.

F - H&K(UC), R&T, Wes.

C - Ber, Gal, Wes.

- E. whitneyi Fosb.
Listed as E. falcata (Gaud.) Gaud. by Christophersen (1927) (See Fosberg, 1939)
C - Ber, SFC, F&M, Lng,
Lepturus repens (Forst. f.) R.Br.
Common in natural and open areas, along roads and in understory where shading is not excessive. This was designated as "Haemoenthua confitessa" on the list of plants collected by Arundel.
P - RCC(K), Bry, J&M, Daw, Lng.
W - Ber, Lng, Wes.
F - Adl(K), Bal, Cht, Wil, H&K(UC), Lng, R&T, Wes.
C - Ber, SFC, F&M, Gal, Ham, Lng, HiF(K), Wes.
- *Panicum maximum Jacq.
Misidentified as P. barbinode Trin.
C - S&F.
- *Paspalum fimbriatum H.B.K.
Dawson (1959) found this naturalized on Cooper islet of Palmyra.
P - Daw.
- *P. orbiculare Forst. f.
Dawson (1959) found this naturalized on Menge islet of Palmyra.
P - Daw.
- *Rhynchelytrum repens (Willd.) C.E.Hubb.
Also known as Tricholaena rosea Nees. Small colony perpetuating itself around Fanning Is. Cable Station.
F - R&T, Wes.
- *Saccharum officinarum L.
Cultivated in village on Washington.
W - observed.
- *Sporobolus indicus (L.) R. Br.
= S. poiretii (R. & S.) Hitch.
On Palmyra Dawson (1959) found naturalized on Menge islet and in disturbed area on Cooper Island and has characteristic large, almost oblong seeds. Another specimen of Sporobolus is in the Bishop Museum with a notation on the label which reads "could be from Palmyra according to Bryan".
P - Daw, Lng.
- *Stenotaphrum secundatum (Walt.) O. Kuntze
Planted as a lawn around Cable Station on Fanning but is spreading somewhat in to waste areas. Included in St. John (1972) list as Brachiaria plantaginea.
F - R&T, Wes.

CYPERACEAE

- *Cyperus compressus L.
A few individuals found in waste area near airport terminal. Perhaps a new introduction.
C - Wes.
- C. javanicus Houtt.
A conspicuous but uncommon sedge on Washington found mainly near wier and in disturbed areas. Also listed as C. pennatus Lamarck.
P - Daw.
W - Ber, Sdg(K), Wes.

*C. kyllingia Endl.

A small colony found in grassy area of village on Washington. Perhaps a new introduction.

W - Wes.

C. polystachyos Rottb.

A common sedge in standing water at fringes of bog and on elevated mounds in bogs of Washington.

P - HiM, Daw, Lng.

W - Ber, Lng, Sdg(K), Wes.

*C. rotundus L.

An uncommon sedge found near habitations.

F - R&T, Wes.

C - SFC, F&M, Sdg(K).

Fimbristylis atollensis St. John

A common sedge found extensively in dry open natural sites and in waste areas around human habitations. Often combined with F. cymosa

R. Br. This is the species which Christophersen listed as

F. spathacea Roth.

P - HiM, Daw, Lng.

W - Ber, Lng, Wes.

F - Bal, Cht, Wil, H&K(UC), R&T, Wes.

C - Ham, Lng, Wes.

Scirpus littoralis Schrader

The dominant species over most of the bog on Washington. Also determined as S. riparius Presl by Streets and Christophersen.

W - Ber, Sdg(K), Wes.

ARECACEAE

*Cocos nucifera L.

Reported in earliest accounts of all the islands but it may have been an aboriginal introduction. Not represented in herbarium collections.

P - observed

W - observed

F - observed

C - observed

*Phoenix dactylifera L.

A few individuals grown in cultivation on Fanning.

F - observed by Wes.

*Livistona chinensis (Jacq.) Mart.

A single specimen by main building of Cable Station on Fanning.

F - observed by Wes.

ARACEAE

*Colocasia esculenta (L.) Schott

Anonymous, 1940, Keyte (1861) and Bryan (1942) reported seeing it in cultivation on Fanning.

F - observed

*Cyrtotheca chamissonis (Schott.) Merr.

Cultivated on Fanning and Washington for food but also naturalized or persisting in bog on Washington. This could also be the "ape" reported by Judd (1859).

W - Ber, Wes.

F - observed

*Scindapsus aureus (Linden ex André) Engl.

= Epipremnum aureum (Linden ex André) Bunting.

It was introduced as an ornamental to Palmyra but has become locally naturalized.

P - Daw.

BROMELIACEAE

*Ananas comosus (L.) Merr.

Bryan (1942) reported seeing it in cultivation on Fanning.

F - observed.

COMMELINACEAE

*Rhoeo spathacea (Sw.) Stearn

A cultivated ornamental on Fanning.

F - R&T, Wes.

LILIACEAE

*Cordyline fruticosa (L.) Chev.

A cultivated species also listed as C. terminalis (L.) Knuth.

W - Wes.

*Gloriosa superba L.

A cultivated ornamental which persists in waste places around Cable Station on Fanning and on Washington.

W - Wes.

F - R&T, Wes.

AMARYLLIDACEAE

*Agave sisalana Perrine ex. Engelm.

A few individuals were observed on Fanning by wharf at Cartwright Point on north side of main pass.

F - observed

*Crinum amabile Donn

Cultivated around Cable Station. Also known as C. augustum Roxb. and C. procerum Herbert and Carey. More material is needed of this plant for study.

F - Wes.

*C. asiaticum L.

A robust species found in cultivation on Washington, Fanning and Christmas.

W - Wes.

F - observed

C - observed

*C. bulbispermum (Burm. f.) Milne-R. & Schw.

Cultivated around Cable Station on Fanning.

F - Wes.

*Hymenocallis littoralis (Jacq.) Salisb.

Cultivated species seen around Cable Station on Fanning. Also known as Pancratium littorale Jacq.

F - Wes.

*Zephyranthes grandiflora Lindl.

Cultivated species on Fanning and Washington which appears to have escaped into waste areas on Washington.

W - Wes.

F - Lng, Wes.

TACCACEAE

*Tacca leontopetaloides (L.) Ktze.

This cultivated species which was observed by Hussey (1841-45), Lucett, (1851), and Bryan (1942) on Fanning. It grows wild on many atolls and could be an aboriginal introduction or may have been brought by the early settlers. It persists in abandoned gardens near Cable Station on Fanning.

F - Wes.

MUSACEAE

*Musa paradisiaca L.

This cultivated species was recorded on Washington at least from 1854 (Holley, 1853-57).

W - observed by Wes.

F - observed by Wes.

C - observed by Wes.

CANNACEAE

*Canna glauca L.

Cultivated in garden of plantation manager on Fanning in 1983.

F - observed by Wes.

CASUARINACEAE

*Casuarina equisetifolia L.

Cultivated trees recorded from all islands.

P - Daw.

W - Wes.

F - R&T, Wes.

C - Lng, Wes.

MORACEAE

*Artocarpus altilis (Parkins.) Fosb.

In cultivation on Fanning, Washington and Christmas but groves were observed on Washington in remote areas which seemed to be reproducing naturally.

W - observed by Wes.

F - R&T, Lng.

C - observed by Wes.

*Ficus carica L.

A cultivated tree on Washington and Fanning.

W - Wes.

F - Adl(K).

*F. prolixa Forst f.

Large, mature trees found along roads and at sites of former camps on Washington.

W - Wes.

F - Adl(K), Wes.

*F. tinctoria Forst. f.

In cultivation around settlements.

F - Wes.

C - Wes.

URTICACEAE

*Pilea microphylla (L.) Liebm.

A widespread naturalized species on Palmyra

P - HiM, Daw, Lng.

Laportea ruderalis (Forst. f.) Chew

Rock (1916) reported it to be abundant on Palmyra at the time of his visit. Common on Fanning and Washington usually in open areas often far from habitations. Also recorded as Fleurya ruderalis (Forst. f.) Gaud. ex Wedd.

P - RCC, Bry, J&M, Lng.

W - Ber, Lng, Sdg(K), Wes.

F - Adl, Bal, Cht, H&K(UC), S&F, Lng, R&T, Lee, Wes.

Pipturus argenteus (Forst. f.) Wedd.

An understory shrub where canopy is open and a colonist in cleared areas.

W - Lng, Sdg(K), Wes.

POLYGONACEAE

*Antigonon leptopus H. & A.

Cultivated in garden around Cable Station on Fanning.

F - Wes.

*Coccoloba uvifera (L.) L.

A cultivated tree observed by Dawson (1959) on Menge, Marine Engineer and Cooper islets of Palmyra where it appears to be naturalized or persisting.

P - HiM, Daw.

AMARANTHACEAE

*Achyranthes aspera L.

= A. indica (L.) Mill.

Presumed to be a naturalized species collected by Arundel but has not been recorded since. There appears to be some confusion between this species and A. indica (L.) Mill.

F - Adl(K).

*Amaranthus viridis L.

An uncommon naturalized herb.

W - Ber, Wes.

NYCTAGINACEAE

Boerhavia tetrandra Forst. f.

Very common on Christmas but present in open areas and disturbed sites on all islands. The taxonomy of this species or group of species needs attention. B. repens L. sensu lato may also be present and the name B. diffusa L. has been misapplied to some specimens from these islands.

P - RCC, Bry, J&M(K), Daw, Lng.

W - Ber, Lng, Wes.

F - Bal, Wil, H&K(UC), Lng, R&T, Wes.

C - Ber(K), Lng, Cur(K), Gri(K), Jen(K), Sdg(K), Wes.

*Bougainvillea sp.

Cultivated and persisting in abandoned gardens. It is unclear to me which species is present.

W - Wes.

F - Wes.

C - observed

*Mirabilis jalapa L.

Found cultivated and as an escape in waste areas near settlements.

W - Wes.

F - R&T,

C - Lng.

Pisonia grandis R.Br.

Forms splendid forests on Fanning, Washington and Palmyra and a few small groves on Christmas.

P - RCC, Cop, Bry, Daw, Lng.

W - Ber, Wes.

F - Wil, H&K(UC), S&F, Lng, Wes.

C - Wes.

AIZOACEAE

Sesuvium portulacastrum (L.) L. var. griseum Deg. and Fosb.

Mat forming species found in areas subject to flooding and high salinity.

F - Adl(K), H&K(UC), R&T, Wes.

C - Str(US), SFC, Gal, Ham, Lng, Wes.

PORTULACACEAE

P. johnii v. Poelln.

A specimen collected by St. John and Cooke from a small island in the lagoon of Christmas Island was among the specimens consulted by von Poellnitz when he described the species (v. Poellnitz, 1936)

C - SFC

P. lutea Soland. ex Forst. f.

Very common on Christmas and in open areas on Fanning.

F - Cht, H&K(UC), R&T, Lee, Sdg(K), Wes.

C - Ber, Wil, SFC, F&M, Gal, Ham, Lng, Wes.

*P. oleracea L.

A cosmopolitan species which, in the Line Islands as elsewhere, is commonly found along roadsides and waste areas. Von Poellnitz (1936) recognized two closely related species, P. fosbergii v. Poelln. and P. johnii v. Poelln., which colonized natural habitats. Fosberg (1943) speculated that P. fosbergii was intermediate between P. oleracea and P. lutea but thought that further study of living material was needed to establish the relationship between these species. Geesink (1969) reduced both P. fosbergii and P. johnii to synonyms. Rock (1916) noted a single plant of what he called P. oleracea on Holei Island of Palmyra atoll but appears not to have collected it. Dawson (1959) found P. oleracea (which he listed as P. fosbergii) which is probably the same species as Rock saw.

P - Daw.

W - Wes.

F - Adl(K), R&T, Wes.

C - F&M, Gal, Ham, Lng, Wes.

ANNONACEAE

*Annona squamosa L.

A cultivated species on Fanning collected by Bergman and also noted by Bryan (1942).

F - Ber.

LAURACEAE

Cassytha filiformis L.

Very common on Christmas and found in a few open habitats on Fanning and Washington.

W - Ber, Wes

F - H&K(UC), R&T.

C - Ber, F&M, Gal, Ham, Wes.

HERNANDIACEAE

*Hernandia sonora L.

= H. nymphaeifolia (Presl) Kub.

This provisional determination is based on sterile material. A few individuals found cultivated on Washington.

W - Wes.

CRUCIFERAE

*Brassica oleracea L.

Cultivated in gardens on Fanning from an early date (Keyte, 1861) and also seen on Washington and Christmas.

W - Wes.

F - observed by Wes.

C - observed by Wes.

Lepidium bidentatum Mont.

Locally common in open habitats and in some artificial clearings. Also recorded as L. owaihiense C. & S. and L. piscidium Forst.

P - Str(US), RCC, J&M, Bry.

W - Ber, Lng, Wes.

F - Adl(K), Cht, H&K(UC), S&F, Lng, R&T, Wes.

C - Cht, Lng.

CRASSULACEAE

*Kalanchoe pinnata (Lam.) Pers.

A cultivated species which persists in abandoned gardens.

F - Long, R&T, Wes.

FABACEAE

*Bauhinia monandra Kurz

St. John (1972) reported that this species was collected by Long but the specimen can not be located.

F - observed

*Caesalpinia pulcherrima (L.) Sw.

A cultivated shrub observed by Russell and Tsuda on Fanning (St. John, 1972).

F - observed

Canavalia carthartica Thouars

Common strand species on Washington. This is the C. microcarpa (DC.) Piper of Christophersen (1927) and probably the C. grandiflora recorded by Streets (1877).

W - [Str], Ber, H&K(UC), Lng, Sdg(K), Wes.

*Cassia occidentalis L.

A volunteer in open areas around settlements.

F - Adl(K), H&K(UC), Wes.

*Crotalaria incana L.

Locally naturalized on Palmyra.

P - Daw, Lng.

*C. retusa L.

Locally naturalized around Napari on Fanning.

F - Wes.

*Crotalaria sp.

One sterile specimen found in waste area on Washington.

W - Wes.

*Delonix regia (Boj.) Raf.

Ornamental in village on Washington.

W - Wes.

*Desmodium triflorum (L.) DC.

Reported to grow along paths in coconut groves by Christophersen (1927).

F - H&K(UC).

*Erythrina variegata L. var. orientalis (L.) Merr.

Christophersen (1927) reported E. indica was grown as an ornamental on Christmas and Bryan (1942) also observed an Erythrina on that island growing around settlements.

C - observed

*Leucaena leucocephala (Lam.) De Wit

Occasionally naturalized in and around settlements. Also reported as L. glauca sensu Hawn. bot. non (L.) Benth.

P - Daw.

W - Lng, Sdg(K), Wes.

F - R&T, Wes.

C - SFC, F&M, HiF.

*Peltophorum pterocarpum (DC.) Backer ex K. Heyne

Large ornamental tree near Cable Station. Sterile specimen misidentified as Jacaranda acutifolia Humb. & Bonpl. (St. John, 1972).

F - R&T, Wes.

*Phaseolus lathyroides L.

One record from Paris on Christmas Island.

C - F&M.

*Trifolium sp.

Sterile plant found in lawn of plantation manager's house on Fanning.

F - Wes.

*Vigna luteola Benth. in Mart.

This plant, which is rare in the Pacific, was found naturalized around Napia village of Fanning Island and was determined by Fosberg.

F - Wes.

ZYGOPHYLLACEAE

Tribulus cistoides L.

Common creeping herb on Christmas.

C - Cht, HiF, Gal, Ham, Wes.

RUTACEAE

*Citrus aurantiifolia (Christm.) Swingle

Cultivated in on Washington and Fanning.

W - Wes.

F - observed

SIMAROUBACEAE

Suriana maritima L.

Common shrub on saline soils on Christmas. Streets (1877a) indicates specimens were collected from Christmas and Palmyra and the plant was "common on all the islands of the Fanning Group" although this is doubtful. One small colony was noted on Fanning in 1982. Small populations may have been missed by recent collectors on Washington and Palmyra or it may be that the species is periodically exterminated but is able to recolonize these two islands.

P - [Str].

F - Wes.

C - Str(US), Ber, Wil, SFC, F&M, Ham, Lng, Sdg, Wes.

EUPHORBIACEAE

*Acalypha wilkesiana Muell. -Arg. in A.DC.

A cultivated shrub in settlements.

P - Lng.

W - Wes.

F - R&T, Wes.

*Breynia disticha Forst. f.

Cultivated shrub on Fanning.

F - Wes.

*Codiaeum variegatum (L.) Bl. var. pictum (Lodd.) Muell.-Arg.

Cultivated shrub in villages.

W - Wes.

F - R&T, Wes.

*Euphorbia glomerifera (Millsp.) L.C.Wheeler

Introduced weed on Palmyra (Dawson, 1959). One plant seen in waste area around village on Christmas. The species identified as E. atoto Forst. f. which appears on the Hill list (Dawson, 1959) is also believed to be E. glomerifera.

P - HiF, Daw.

C - Wes.

*E. heterophylla L. var. cyathophora (Murr.) Griseb.

Common around Cable Station on Fanning and in disturbed areas on other islands. Also known as E. cyathophora Murr.

P - HiM, Daw.

W - Wes.

F - R&T, Wes.

C - Wes.

*E. hirta L.

Common weed in waste areas and along roadsides.

P - [HiM].

W - Ber, H&K(UC), Wes.

F - Bal, H&K(UC), R&T, Wes.

C - Ber, F&M, Sdg(K), Pry(K), Wes.

*E. prostrata Ait.

Common weed in waste areas and heavily disturbed sites.

W - Ber, Sdg(K), Wes.

F - H&K(UC), Lee.

C - Wes.

*Manihot esculenta Crantz

Cultivated in villages.

W - Wes.

F - R&T.

*Phyllanthus amarus Schum.

Common weed misidentified as P. niruri L. (Christophersen, 1927) and as P. debilis Klein ex Willd. (Dawson, 1959).

P - Daw.

W - Ber, H&K(UC), Wes.

F - Bal, Cht, H&K(UC), R&T, Wes.

C - Ber, F&M.

ANACARDIACEAE

*Mangifera indica L.

Cultivated in settlements on Fanning and Washington.

W - Wes.

F - observed by Wes.

TILIACEAE

Triumfetta procumbens Forst. f.

Native to Polynesia, Micronesia and Malaya (Neal 1965) and used for fiber, ornament, magic and medicine (Luomala, 1953). Probably native to the Northern Line Islands but conceivably a human introduction.

P - Daw, Lng.

W - Lng.

F - Adl(K), Bal, H&K(UC), R&T, Lee, Wes.

MALVACEAE

*Abutilon albescens Miq.

Locally abundant on Christmas. Wrongly identified as A. indicum Sweet (Fosberg, 1943).

C - F&M.

*Hibiscus rosa-sinensis L.

Cultivated and persisting around settlements on Washington, Fanning and Christmas.

W - Wes.

F - Wes.

C - observed by Wes.

*Hibiscus tiliaceus L.

Cultivated and escaped around settlements.

P - HiM, Daw.

W - Wes.

C - Ber, F&M, Ham, Wes.

*Malvastrum coromandelianum (L.) Garcke.

Naturalized in waste areas.

W - Ber, Wes.

F - H&K(UC), Wes.

Sida fallax Walp.

One of the most common shrubs on Christmas. Streets (1877a) recorded it as S. dielli Gray, which is probably the same, and Christophersen (1927) misidentified it as S. cordifolia.

F - Adl(K), Bal(K), H&K(UC), R&T.

C - Str(US), HiF, Wes.

*S. rhombifolia L.

In disturbed habitats around settlements.

W - Ber, Wes.

C - Ber.

STERCULIACEAE

*Waltheria indica L.

Also known as W. americana L. One colony found near Cable Station, perhaps a new arrival.

F - Wes.

GUTTIFERAE

*Calophyllum inophyllum L.

Cultivated trees around villages.

P - Daw.

W - Wes.

F - Cht, Wes.

PASSIFLORACEAE

*Passiflora foetida L.

Weed around Cable Station on Fanning.

F - R&T, Wes.

CARICACEAE

*Carica papaya L.

Cultivated in settlements of Washington, Fanning and Christmas and mostly used for pig food.

W - Wes.

F - Wes.

C - observed by Wes.

COMBRETACEAE

*Terminalia catappa L.

Cultivated around settlements.

P - Daw.

W - Wes.

F - Wes.

C - observed by Wes.

MYRTACEAE

*Psidium guajava L.

Cultivated around settlements.

W - Ber, Wes.

F - Wes.

ONAGRACEAE

Ludwigia octovalvis (Jacq.) Raven

Found in flooded substrate near lake on Washington.

P - Him, Daw.

W - Lng, Wes.

ARALIACEAE

*Polyscias fruticosa (L.) Harms

Cultivated in gardens.

W - Wes.

*P. guilfoylei (Bull) Bailey

Cultivated in gardens.

F - S&F, R&T, Wes.

*P. scutellaria (Burm. f.) Fosberg

Cultivated in gardens.

W - Wes.

F - R&T, Wes.

OLEACEAE

*Ligustrum sp.

The specimen collected by Russell and Tsuda (St. John, 1972) can not be located in the Bishop Museum. It may have been redetermined or lost.

F - [R&T]

APOCYNACEAE

*Nerium oleander L.

Cultivated and persisting in abandoned gardens.

F - R&T, Wes.

C - observed by Wes.

Ochrosia oppositifolia (Lam.) K. Schum.= Neisosperma oppositifolia (Lam.) Fosb. and Sachet.

Found only near west end of Holei islet of Palmyra.

P - Him, Daw.

*Plumeria obtusa L.

Cultivated as ornamental and used in leis. Observed on Washington, Fanning and Christmas.

W - Wes.

F - observed by Wes.

C - observed by Wes.

*P. rubra L. forma rubra

Cultivated as ornamental and used in leis.

W - Wes.

F - observed by Wes.

C - observed by Wes.

(P. rubra)

forma acutifolia (Poir.) Woodson

Cultivated as ornamental and used in leis. Probably also on Christmas.

W - Wes.

F - Wes.

ASCLEPIADACEAE

*Asclepias curassavica L.

An introduced weed which was collected by Arundel last century but not recorded since.

F - Adl(K).

CONVOLVULACEAE

Cuscuta campestris Yuncker

Common at South East Point of Christmas Island and occasionally between small ponds (Garnett, 1981).

C - Lng, Wes.

*Ipomoea batatas (L.) Poir.

Cultivated in village on Washington in 1854 (Holley, 1853-57). Now found cultivated and growing along nearby roadsides.

W - Wes.

I. pes-caprae ssp. brasiliensis (L.) v. Ooststr.

A pioneer on beaches and in open sites.

P - Daw, Lng.

W - Ber, H&K(UC), Wes.

F - R&T, Wes.

I. macrantha R. & S.

Recorded also as I. tuba (Schlecht.) G. Don, I. grandiflora (Choisy) Hall f. and I. glaberrima Bojer. A common vine on Fanning and locally abundant on Washington.

P - Bry, Daw.

W - Ber, Wes.

F - S&F, Lng, R&T, Wes.

*Merremia dissecta Hallier

In Cable Station garden on Fanning and identified by the author.

F - Wes.

BORAGINACEAE

*Cordia sebestena L.

Cultivated tree in London village on Christmas.

C - Wes.

C. subcordata Lam.

In scattered locations usually not far from beach. On Washington it seemed to be associated with fresh water seeps.

W - Ber, Wes.

F - Bal, R&T, Lee, Wes.

Heliotropium anomalum (H. & A.) var. mediale Johnst.

Very common on Christmas an in open sites on Fanning.

F - Adl(K), Bal, Cht, Wil, H&K(UC), S&F, R&T, Sdg(K), Lee, Wes.

C - Ber, Wil, SFC, F&M, Gal, Ham, Jen, Cur, HiF, Gri, Wes.

Tournefortia argentea L. f.

Typically a string of these trees is found along the top of the beach. Also recorded as Messerschmidia argentea (L.f.) Johnst.

P - RCC, Bry, J&M.

W - Ber, H&K(UC), Wes.

F - Bal, H&K(UC), Wes,

C - Ber, SFC, F&M, Ham, Lng, Wes.

VERBENACEAE

*Clerodendrum inerme (L.) Gaertn.

A favored ornamental grown as a hedge and for its flowers which are used in leis. It has become established at a number of sites in the bog on Washington.

W - Sdg(K), Wes.

F - S&F, Lng, R&T, Sdg(K), Wes.

*Lantana camara L.

Cultivated in villages where flowers are used in leis.

W - Wes.

F - R&T.

*Premna obtusifolia R. Br.

Cultivated in village on Washington.

W - Wes.

*Stachytarpheta urticaefolia (Salisb.) Sims

Apparently common on Palmyra and found once on Fanning.

P - HiM, Daw, Lng.

F - R&T.

*Vitex trifolia L.

Cultivated around Cable Station on Fanning and persists on Palmyra and is the same as V. negundo var. bicolor (Willd.) H. Lam (Dawson, 1959).

P - HiM, Daw.

F - Wes.

LABIATAE

*Ocimum basilicum L.

Cultivated in gardens

F - S&F.

SOLANACEAE

*Capsicum annuum L.

Cultivated in settlements. Persists for a while after garden has been abandoned.

W - observed by Wes.

F - Wes.

C - observed by Wes.

*Lycopersicon esculentum Mill.

= Solanum lycopersicum L.

Cultivated on Fanning and Christmas but volunteers were noticed in waste areas on Christmas.

F - observed by Wes.

C - Lng, Wes.

*Nicotiana tabacum L.

Cultivated and able to resist attacks by land crabs.

F - Adl(K).

C - observed by Wes.

*Physalis minima L.

A volunteer in disturbed areas; determined by D. Symon.

W - Wes.

C - Wes.

SCROPHULARIACEAE

*Russelia equisetiformis Schlecht. & Cham.

A cultivated species which is able to persist after abandonment of garden.

W - Wes.

F - Lng, R&T, Wes.

BIGNONIACEAE

*Spathodea campanulata Beauv.

Cultivated tree on Washington and Fanning.

W - Wes.

F - observed by Wes.

*Tecoma stans (L.) Juss. ex B.& H.

Also known as Stenolobium stans (L.) D. Don and prized for its flowers.

W - Wes.

F - R&T, Wes.

ACANTHACEAE

*Blechnum brownei Juss.

Dawson (1959) recorded the species Blechnum brownei. This is assumed to be a typographical error since no fern by this name can be found and the species was listed with other Acanthaceae. The specimen could not be located in the Bishop Museum where Dawson's specimens are preserved.

P - [Daw].

*Graptophyllum pictum (L.) Nees ex Griff.

Said to be persisting on Palmyra (Dawson, 1959).

P - [Daw]

*Pseuderanthemum carruthersii (Seem.) Guillaum.

A common cultivated ornamental around settlements.

P - Daw.

W - Wes.

F - Lee, Wes.

C - Wes.

RUBIACEAE

*Spermacoce assurgens R. & P.

Also listed as S. suffrutescens Jacq. and misidentified as Borreria laevis (Lam.) Griseb. A common weed in disturbed areas and along roadsides.

P - Daw.

W - Sdg(K), Wes.

F - S&F, Lng, R&T, Wes.

*Gardenia taitensis DC.

Cultivated on Washington and Fanning but not common.

W - Wes.

F - observed by Wes.

*Guettarda speciosa L.

Cultivated around villages for fragrant flowers which are used in leis. The plant appears to volunteer around margins of settlements. It was once collected on Palmyra (Dawson, 1959). Could be native to the Line Islands.

P - [HiM].

W - Wes.

F - Wil, S&F, R&T, Lee, Wes.

C - Lng.

Hedyotis romanzoffiensis (C. & S.) Fosb.

A few populations found on Christmas in vicinity of ponds and lagoons.

C - Ber, SFC, F&M, Lng, Wes.

*Morinda citrifolia L.

Found mostly in disturbed areas around villages and a few natural sites. Probably introduced but could be native to these islands.

W - Ber, Lng, Wes.

F - Bal, R&T, Wes.

C - observed by Wes.

CUCURBITACEAE

*Cucurbita pepo L.

Reported to be cultivated on Fanning in 1840 (Anonymous, 1838-41).

Now found in villages on Washington, Fanning and Christmas.

W - observed by Wes.

F - Wes.

C - observed by Wes.

*Citrullus lanatus Schrad. in Ecklon and Zeyher.

Reported on Fanning in 1840 (Anonymous, 1838-41).

F - observed by Wes.

GOODENIACEAE

Scaevola sericea Vahl

Recorded also by synonyms S. taccada (Gaertn.) Roxb. and S. koenigii Vahl. Streets misidentified it as S. plumieri (L.) Vahl. This common strand shrub forms dense thickets on Fanning and Christmas Island. It occurs in a few patches on Washington and is a colonist of disturbed habitats on Palmyra (Maragos, 1979).

P - J&M, Bry, HiM.

W - Ber, Wes.

F - Bal, H&K(UC), S&F, Wes.

C - Str(US), Ber, SFC, F&M, Gal, Ham, Wes.

ASTERACEAE

*Bidens pilosa L.

A weed in disturbed areas around settlements.

W - Lng, Wes.

F - S&F, R&T, Sdg(K), Wes.

*Emilia sonchifolia (L.) DC.

An occasional volunteer on Palmyra.

P - Daw.

*Erechtites hieracifolia (L.) Raf.

This introduced weed was misdetermined as E. valerianaefolia (Wolf) DC. and appeared in the Dawson (1959) list under that name. It has since been redetermined by Fosberg as the closely related E. hieracifolia.

P - HiM.

*Erigeron bonariensis L.

=Conyza bonariensis L.

The E. canadensis L. which appeared in the Dawson (1959) list has been redetermined as E. bonariensis. This is probably the same as the E. albidus (Willdenow) A. Gray recorded by Christophersen (1927) on Fanning.

P - HiM, Daw.

F - H&K(UC).

*Gaillardia pulchella Foug.

An ornamental which has volunteered extensively around the Cable Station on Fanning.

F - R&T, Wes.

*Pluchea indica (L.) Less.

Present on Palmyra and found in a few locations on Christmas.

P - Bry, HiM, Daw.

C - Ham, Sdg(K), Wes.

*P. X fosbergii Cooperider & Galang

This hybrid can often be found where P. indica and P. odorata grow together.

P - HiM, Daw, Lng.

C - Lng.

*P. odorata (L.) Cass.

= P. symphytifolia (Mill.) Gillis

Forms dense stands on Christmas in disturbed areas. The specimen collected by Hill in 1949 and reported by Dawson (1959) has been redetermined as X P. fosbergii.

P - Lng.

F - R&T, Wes

C - Gal, Ham, Lng, Jen(K), Gri(K), Sdg(K), Wes.

*Sonchus oleraceus L.

Christophersen (1927) noted it around Cable Station on Fanning.

F - [Bal]

*Synedrella nodiflora (L.) Gaertn.

A common weed in disturbed areas.

P - HiM, Daw, Lng.

W - H&K(UC), Sdg(K), Wes.

F - Bal, H&K(UC), R&T, Wes.

*Tridax procumbens L.

A local population found near Captain Cook Hotel on Christmas Island. May be a recent arrival.

C - Wes.

*Verbesina encelioides (Cav.) B. & H. ex Gray

A volunteer around London village on Christmas.

C - Wes.

*Vernonia cinerea (L.) Less.

A common weed along roadsides and around settlements.

P - Daw, Lng.

W - Ber, H&K(UC), Wes.

F - Bal, Cht, H&K(UC), R&T, Wes.

C - Ber, Wes.

BIBLIOGRAPHY

Anonymous, 1838-41, Log of the USS Peacock, Pacific Manuscripts Bureau
Doc. 773.

-----, 1874-86, Pacific Islands: Arundel, Plant Lists, Tropical Asia,
Australasia and Southern Islands, 1874-86, Volume 14, bound volume of
determination lists in Royal Botanical Gardens, Kew.

----- (Marie-Helene Sachet?), 1962, The Natural History Society
(Christmas Island) and its Bulletin, Atoll Research Bulletin, 94:1-5.

Arundel, John T., 1870-1919, Diary, Pacific Manuscript Bureau
manuscript nos. 480-492.

-----, 1890, Phoenix Group and other islands of the Pacific. New
Zealand Herald, 5 and 12 July, Auckland.

Bailey, Eric, 1977, The Christmas Island story, Stacey International,
London.

Ball, S. C. (n.d.), Field note books, manuscript in the library of the
Bernice P. Bishop Museum.

Bennett, Frederick D., 1970, Narrative of a whaling voyage round the
globe from the year 1833 to 1836, 2. vols., N. Israel, Amsterdam and
Da Capo, New York (facsimile of 1840 edition published by Richard
Bentley, London).

Brown, F.B.H., 1930, New Polynesian plants, Occasional Papers Bernice
P. Bishop Museum, 9:1-23.

-----, 1931, Flora of southeastern Polynesia, Bulletin Bernice P.
Bishop Museum, 84.

Bryan, Edwin H. Jr. 1942, American Polynesia and the Hawaiian chain,
Tongg Publishing Co., Honolulu.

-----, 1974, Panala'au memoirs, Bernice P. Bishop Museum, Honolulu.

Carter, John (Ed.), 1984, Pacific Islands yearbook, Pacific
Publications, Sydney.

Chock, Alvin, 1963, J. F. Rock, 1884-1962, Taxon, 12:89-102.

- and Dean C. Hamilton, 1962, Plants of Christmas Island, Atoll Research Bulletin, 90.
- Christophersen, Erling, 1927, Vegetation of Pacific equatorial islands Bulletin Bernice P. Bishop Museum, 44.
- Dawson, E. Yale, 1959, Changes in Palmyra Atoll and its vegetation through the agency of man, 1913-1958, Pacific Naturalist, 1:1-51.
- English, John, 1857, Letter to William Miller H.B.M. Consul General in the Pacific Ocean, Foreign Office Document, 58/85 Miller No. 14.
- Fosberg, F. R. 1939, Notes on Polynesian grasses , Occasional Papers Bernice P. Bishop Museum, 15:37-48.
- , 1943, Notes on the plants of the Pacific atolls III, a brief summary, Bulletin Torrey Botanical Club, 70:386-397.
- , 1953, Vegetation of Central Pacific atolls, a brief summary, Atoll Research Bulletin, 23.
- Gallagher, M. D., 1960, Bird notes from Christmas Island, Pacific Ocean, The Ibis, 102:489-502.
- Garnett, Martin, 1981, Christmas Island wildlife sanctuary: Information to visitors, Wildlife Conservation Unit, Christmas Island, mimeo.
- Geesink, R., 1969, An account of the genus Portulaca Indo-Australia and the Pacific, Blumea, 17:275-301.
- Greene, Daniel B., 1860-65, Log of the Massachusetts, Pacific Manuscripts Bureau, Doc. 349.
- Gregory, Herbert E., 1923, The report of the Director for 1923, Bulletin Bernice P. Bishop Museum, 4.
- , 1925, The report of the Director for 1924, Bulletin Bernice P. Bishop Museum, 24.
- , 1935, The report of the Director for 1934, Bulletin Bernice P. Bishop Museum, 133.
- Hemsley, William Botting, 1855, List of the plants collected in the Pacific Islands by J.T.Arundel, Report on the scientific results of the voyage of the H.M.S. Challenger. Botany Vol. 1, Part 4, p. 116.
- Herms, William B., 1925, Entomological observations on Fanning and Washington Islands, together with general biological notes, Pan-Pacific Entomologist, 2:49-54.
- , 1926, Diocalandra taitensis (Guerin) and other coconut pests of Fanning and Washington Islands, Philippine Journal Science, 30:243-271.

- Holley, Richard, 1853-57, Log of the Washington, Pacific Manuscripts Bureau, Doc. 369.
- Holtum, R.E., 1974, Asplenium Linn. sect. Thamnopteris, Gardener's Bulletin, 27:143-154.
- Jenkin, R. N. and M. A. Foale, 1968, An investigation of the coconut growing potential of Christmas Island, Directorate of Overseas Surveys, Land Resources Division (Land Resource Study, 4), Tolworth, England, 2 vols.
- Judd, G. P., 1859, Journal of G.P. Judd, Hawaii Mission Childrens Library, Honolulu.
- Hussey, Benjamin R., 1841-45, Log of the James Maurey, Pacific Manuscripts Bureau, Doc. 365.
- Keyte, G.S., 1861, Fanning's Island: An incident, The Friend, 18:31.
- Kondo, Y. and William J. Clench, 1952, Charles Montague Cooke Jr.: A bio-bibliography, Special Publication, Bernice P. Bishop Museum, 42.
- Langdon, Robert, 1974, Arundel, the shy Cecil Rhodes of the Pacific Islands, Pacific Islands Monthly, 45:59-61.
- Lanjouw, J. and F.A. Staflen, 1954, Index Herbariorum Part II, Collectors A-D, Regnum Vegetabile 2, International Bureau for Plant Taxonomy and Nomenclature, Utrecht, Netherlands.
- Loomis, Elisha and Maria, 1820-24, Extracts from the journal of Elisha and Maria Loomis, typescript in Hawaii Mission Childrens Library, Honolulu.
- Loomis, Maria, 1820-24, Journal of Mrs. Maria Sartwell Loomis, typescript in Hawaii Mission Childrens Library, Honolulu.
- Luomala, Katherine, 1953, Ethnobotany of the Gilbert Islands, Bulletin Bernice P. Bishop Museum, 213,
- Lucett, Edward, 1851, Rovings in the Pacific from 1837 to 1849, 2 vols., Longman, Brown, Green and Longmans, London.
- Maragos, James E., 1979, Palmyra Atoll: Preliminary environmental survey and assessment, U.S. Army Corps of Engineers, Honolulu.
- Martelli, V., 1926, A new species of Pandanus from Fanning Island, University of California Publications in Botany, 13:145-146.
- Merrill, E.D., 1925, On the flora of Fanning and Washington Islands, Christophersen referred to this manuscript when preparing his study of the vegetation of the Central Pacific atolls and stated that it was on file in the Library of the Bernice P. Bishop Museum. No trace can be found of it there.

- Ministry of Education Training and Culture, Kiribati Government, 1979, Kiribati: Aspects of history, published jointly with Pacific Studies and Extension Services, University of the South Pacific, Tarawa, Kiribati.
- Neal, Marie C., 1965, In gardens of Hawaii, Bernice P. Bishop Museum Press, Honolulu.
- Poelnitz, Karl von, 1936, New species of Portulaca from southeastern Polynesia, Occasional Papers, Bernice P. Bishop Museum, 12:1-6.
- Republic of Kiribati, 1983, Resources Study of Fanning and Washington (Northern Line Islands), mimeographed government report, 63 pp.
- Rock, Joseph F., 1916, Palmyra Island: with a description of its flora, Honolulu Star Bulletin, Honolulu.
- , 1929, The voyage of the Luka to Palmyra Island, Atlantic Monthly, 144:360-366.
- Skerrett, Joseph S., 1873-4, Log of the U.S.S. Portsmouth, manuscript in the U.S. National Archives, Washington D.C.
- Sledge, W. A. 1984, University of Leeds, personal communication.
- Stone, Benjamin C., 1968, Notes on Pandanus in the Line Islands, Micronesica, 4:85-93.
- St. John, Harold, 1952, A new variety of Pandanus and a new species of Fimbristylis from the Central Pacific Islands. Pacific Plant Studies 11, Pacific Science, 6:145-150.
- , 1974, The vascular flora of Fanning Island, Line Islands, Pacific Ocean, Pacific Science, 28:339-355.
- Streets, Thomas H., 1876, Description of a new duck from Washington Island, Bulletin Nuttall Ornithological Club, 1:46-47.
- , 1977a, Contributions to the natural history of the Hawaiian and Fanning Islands and Lower California made in connection with the U.S. North Pacific Surveying Expedition 1873-75, Bulletin of the U.S. National Museum, 7.
- , 1877b, Some account of the natural history of the Fanning group of islands, American Naturalist, 11:65-72.
- Updike, John, 1973, Pigeon feathers and other stories, Knopf, New York.
- Wentworth, Chester K. 1925, A tropical peat bog, Bulletin Geological Society of America, 36:137.

-----, 1931, Geology of the Pacific equatorial islands, Occasional Papers Bernice P. Bishop Museum, 11.

Wilkes, Charles, 1970, Narrative of the U. S. Exploring Expedition, 5 vols., Gregg Press, Upper Saddle River, New Jersey, (facsimile of first edition published in 1845).

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COMMUNITY STRUCTURE OF REEF-BUILDING
CORALS IN THE FLORIDA KEYS: CARYSFORT REEF,
KEY LARGO AND LONG KEY REEF, DRY TORTUGAS

BY

PHILLIP DUSTAN

ISSUED BY

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COMMUNITY STRUCTURE OF REEF-BUILDING
CORALS IN THE FLORIDA KEYS: CARYSFORT REEF,
KEY LARGO AND LONG KEY REEF, DRY TORTUGAS

By

PHILLIP DUSTAN 1/

The reefs of the Florida Keys are widely known and have drawn the attention of scientists since the early 1800s. The landmass of the Keys are the fossil remains of Pleistocene reefs (Hoffmeister and Multer, 1964). Their species composition can be seen in nearly every canal cut and rock quarry (Hodges, 1977). Receiving less attention however, are the reefs that make up the present living chain of reefs from Fowey Rocks south to the Dry Tortugas. These reefs are distributed in and along the outer edge of the shallow lagoon on the seaward side of the Keys. There are hundreds of individual reefs in the Keys, however there are less than 25 that could be considered to be more than patch reefs. The largest, most well-developed outer reefs presently are, in north-south order: Carysfort, Molasses, Looe Key, the Sambos, Long Key, and Loggerhead Reefs. Looe Key, Carysfort, Molasses and Long Key Reefs are similar in that they have rich coral communities which exhibit species zonal patterns similar to other Caribbean reefs (e.g. Goreau, 1959), and a topographic relief that appears to be the result of active coral growth on top of older reefs or eolian dune systems (Shinn 1963, 1977, 1980). Rates of reef accretion are greatest in the region of Key Largo and the Dry Tortugas (Shinn 1977). Although they exist at the northern and southernmost ends of the Florida Keys, Carysfort Reef, Key Largo and Long Key Reef in the Dry Tortugas are the most similar of the large reefs. Each is exposed to prevailing seas and has approximately the same depth range and species composition.

This communication is the result of two parallel studies on the distribution of reef-building corals on Carysfort Reef, Key Largo and Long Key Reef, Dry Tortugas. The aim of the projects was to characterize the species composition of reef-building corals from the northern and southernmost localities of the Keys, establish base line data for future studies, and, through comparison, attempt to identify the impact of man on the reefs in the Key Largo area of the northern Florida Keys. Participants in the project include K. Lukas, J. Thompson, D. Girardin, K. Gordon, J. Halas, C. Richardson. Other contributors included J. W. Japp and J. Wheaton-Smith from the Department of National Resources, State of Florida, and G. Davis of the National Park Service. All assisted in phases of the field work and all are due grateful thanks. This research was supported by the Smithsonian Institution and Harbor Branch Foundation with logistical support in the Dry Tortugas provided by The National Park Service.

METHODS

There are many stages of reef development and community complexity in both the Key Largo and Tortugas areas. The sites were chosen for their exposure to the prevailing seas and the general lushness of reef community as observed in aerial photographs and preliminary SCUBA excursions to each reef. As the long range goal of the project was to provide baseline data for both areas, the most information on the organization of the reef communities could be gathered in short time periods at the richest areas. Furthermore, should changes occur in the species composition of either reef, it might be most readily detectable in the areas of highest coral coverage and species diversity, as there is some suggestion that the most complex regions of ecosystems may be the most susceptible to environmental perturbation (Margalef, 1963). Carysfort Reef was surveyed in the spring of 1975 and Long Key in July 1975.

The abundance and species composition of the coral community was estimated using line transects (Loya, 1972). This technique estimates projected surface-area coverage. It is biased in that flat colonies will project more surface area than round colonies which are spherical in skeleton morphology but not in tissue coverage (Porter, 1972). The upper surfaces of most colonies however, are covered with tissue, while their sides are often not. The error introduced by not using the chain method is probably 2-3 percent. However, the reduction in underwater working time afforded by the line transect allowed us to undertake a project of this magnitude in the relatively short period of time we had available. If one colony overlapped another, each colony was measured and recorded sequentially. This was not common in most parts of the reef with the main exception being the regions of profuse Acropora cervicornis growth on Carysfort Reef and the sides of the surge channels on Long Key Reef.

The length of transects used to measure coral abundance was determined by running two 50 meter long transects on the fore-reef terrace of Carysfort Reef at a depth of 17 meters. The species that the line crossed were recorded for each successive meter and a species area curve derived. The data (Fig. 1) show that the species area curve reaches its asymptote in the first twenty meters. A measurement transect length of twenty-five meters was chosen as optimal and used throughout the two study areas. (For more details see Loya, 1972).

On both reefs, measurement transects were positioned along a reference line set from the surface. A single long line was stretched from the deepest point of the reef to the shallow reef flat. Measurement transect lines (25m in length) were placed perpendicular to this line creating a grid of transects that paralleled the reef flat and the prevailing swell. The interval between measurement transects varied from 3 to 20 meters depending on the coral coverage and reef geomorphology. In areas of extremely steep slope the lines were spaced at three meter intervals, ten meters in regions of high coral coverage, and twenty meters apart in zones of very low coverage.

Carysfort Reef

Carysfort Reef (Fig. 2.) consists of two parallel platforms tangential to the prevailing seas. The inner platform is densely covered with living reef corals, while the outer platform supports a much reduced population of hermatypes. Seaward of the outer platform, fathometer recordings show small knolls between 25-35m. At forty meters there is a sill 3-4m high which is colonized by reef-building coral communities consisting mostly of Agricia spp. and Montastrea spp. (Dustan, Girardin, and Halas, unpublished observations). The angle of the slope increases seaward of this deep sill and the bottom drops off into the Straits of Florida.

The study site is situated on the inner terrace of Carysfort Reef, approximately 75 meters south of the Carysfort lighthouse. The transect line runs on a compass bearing of 100 degrees magnetic from behind the reef flat to the edge of the first terrace at 20 meters. The inner terrace is approximately 250 meters wide and exhibits zonal patterns in the distribution of the reef-building corals that resemble the zonal patterns described for Jamaica (Goreau, 1959) and the Bahamas (Storr, 1964). Zones occur in a series of successive bands parallel to the reef flat and thus perpendicular to the direction of the prevailing seas. The zonal patterns are not as well defined as in Jamaica and there is considerable patchiness in the distribution of species. The study area contains six zones based on changes in species composition and morphology (Fig. 3., Table 1). From behind the reef towards the Straits of Florida these are:

1. Back reef
2. Reef flat
3. Acropora palmata zone
4. Gorgonian zone
5. Fore-reef terrace
6. Fore-reef escarpment

The terminology used here is modified from Goreau (1959) and Kinzie (1973). This ecological zonation scheme is similar to that proposed for Key Largo Dry Rocks (Shinn 1963) and Grecian Rocks (Shinn 1980).

Carysfort Reef Zonation

The inshore limit of Carysfort Reef, the back reef, is characterized by low coral coverage on a coarse sand bottom. Small outcrops of Montastrea annularis and Acropora cervicornis are colonized by encrusting Porites astreoides and Agaricia agaricites. The sand bottom interdigitates with the lee side of the reef flat. In some places there is an abrupt change between the two areas and in others the transition is more gradual. These ecotone areas are inhabited by large M. annularis colonies and groves of A. cervicornis. Along the irregular backside edge of the reef flat there are large colonies of Acropora palmata. Some colonies are overturned suggesting occasional heavy storm damage.

The reef flat is approximately 50 meters wide and tabletop flat. It is covered with Acropora palmata and red crustose coralline algae, and is similar, but more expansive, than the reef flats of the inner reefs Grecian and Key Largo Dry Rocks (Shinn 1963, 1980), and those described for St. Croix by Adey (1975). The frame is constructed of densely packed dead Acropora palmata colonies in growth position which are encrusted with red crustose coralline algae. Other reef building species, mainly Porites astreoides, Agaricia agaricites, and Acropora cervicornis inhabit hollows that place them below the mean height of the reef flat. The structure of the reef flat appears dense but is riddled with narrow tunnels beneath the branches of the dead Acropora palmata framework. The seaward edge of the reef flat grades into irregular groves of Acropora palmata that suggest the beginnings of a spur and groove structure. In places the colonies are dense and overlap extensively, often overgrowing one another (Photo A). This region is the region of greatest wave activity on the reef. Close to the reef flat the tips of the Acropora palmata branches are level with the reef table and gradually deepen seaward. Further seaward, coral coverage decreases and the Acropora palmata colonies become oriented into long spurs that jut into the open sea (Shinn, 1963). Irregular sand channels run between the spurs with relief between the channel floors and top of the spurs approaching 2-3 meters in places. Coral rubble, mostly Acropora palmata, is strewn along the channels between the spurs.

Interspersed with the Acropora palmata community are patches of the hydrozoan Millepora complanata in association with Porites astreoides, Favia fragum, the Gorgonia ventalina, and carpets of the zooanthid Palythoa spp. The blades of the Millepora colonies are oriented predominantly tangential to the prevailing seas with blades occasionally offset at right angles. This species association is analogous to the sea fan zone described by Storr (1964) for the Bahamas and occurs mostly on the tops of the Acropora palmata spurs and reef rock to a depth of approximately four meters. Millepora complanata is very abundant on the tops of the outcrops, comprising over 80% of the total coral coverage or over 45% of the reef substrate. This area is similar to the Millepora-Montastrea zone on Dry Rocks (Shinn, 1963) but more spread out and not as well organized.

Seaward of the Acropora palmata zone there is a trough that is approximately 25 meters wide. The bottom consists mostly of hard reef rock covered with gorgonians and reef corals. Coral coverage in this trough drops to an estimated 20%. The morphology of the corals and rock coverage are similar to the shallow barren zone described by Kinzie (1973) for the reefs of Discovery Bay, Jamaica and appears analogous to Shinn's Rubble zone of the inner reefs (Shinn, 1963, 1980). Seaward of the trough is a broken line of reef rock forming an irregular ridge which has a relief of 2-3 meters. This ridge parallels the reef crest and is dissected by numerous small channels and breaks. In a few places, the ridge takes on the appearance of the shallower spur and groove system of the Acropora palmata zone. The top and seaward side of the ridge supports a large sea fan community

(Storr, 1964). Millepora complanata covers 48% of the reef substrate at the transect site. Other species include an occasional large colony of Montastrea cavernosa, M. annularis, and Colpophyllia natans. This ridge system terminates abruptly on the seaward side in an area of sparse coral coverage and the gorgonian zone begins.

Unlike the region just described, the gorgonian zone has a sparse cover of small hemispherical colonies of Porites astreoides, and Dichocoenia stokesii and supports a rich and diverse community of gorgonians and algae (Photo B). The sea-fan-Millepora complanata species complex is virtually absent. The substrate is hard reef rock of very low relief which allows settlement of gorgonians (Kinzie, 1973) which include members of Pterogorgia, Pseudoptergorgia and Eunicia. There are no surge channels or buttress features.

Occasionally situated on this flat, gently sloping plane are large colonies of Montastrea annularis. In the transect area one such colony approached 7 meters in diameter and 3 meters in height. This colony sheltered a fish cleaning station and was the center of focus of the local fish population (Photo C). At a depth of nine meters the gorgonian zone terminates sharply with the sudden occurrence of Acropora cervicornis colonies. Coral coverage changes from less than 10% to over 25% in less than 3 meters horizontal distance (Photo D). The presence of these Acropora cervicornis marks the beginning of the fore-reef terrace population, an area of high species diversity and coverage. Just seaward of the gorgonian zone the community is dominated by Acropora cervicornis, Montastrea annularis, and Colpophyllia natans. Further seaward, the dominant species change to Stephanocoenia michelinii, Montastrea annularis, and Mycetophyllia ferox. This species assemblage in turn is replaced by a Siderastrea siderea dominated community on the fore-reef escarpment. Submarine light levels on the fore-reef terrace are relatively low due to turbidity (visibility is usually less than 17-18m).

The morphology of the fore-reef slope is irregular with corals, gorgonians, and sponges occupying reef rock knolls separated by small patches of fine sediment. Most of the hermatypic corals grow upwards off the sediment covered bottom and then increase in surface area. This creates tall, slightly expanding cylindrical coral mounds between 0.5 and 1 meter above the soft, fine sediment covered bottom. In some instances the pillars are formed by a single coral colony and in others a few colonies, making the mound similar to a multiscoop ice cream cone. The sides of these coral build-ups are colonized by small corals, encrusting gorgonians, sponges, and bryozoa in addition to a rich and diverse algal community. Biological erosion appears to be intense and many of these pillars topple easily when jarred. These mounds vary in size and often coalesce when the edges of living coral colonies meet. This coalescence gives the reef the appearance of being much more solid than it really is and adds tremendously to the geometric complexity of the internal framework structure. Toward the escarpment the pillars are more isolated, rise higher off the bottom, and the reef framework even less solid.

The escarpment marks the end of the fore-reef terrace. In places it is a vertical drop of slightly over five meters and in others a steep slope. Coral capped reef rocks overhang the steeper edges. Collapsed overhangs and slump block features are common (Photo E and F). In some areas large talus piles of reef rock cover the soft bottom at the base of the escarpment, and in other places the reef gradually grades into a soft, fine sediment substrate. On a large scale the escarpment appears to be irregularly buttressed. The buttresses seem to be constructed by reef-building corals growing on old slump blocks and reef debris. These buttress features are approximately 30 meters apart. Seaward of the escarpment is a soft fine sediment covered bottom that stretches flat some 100 meters to the beginning of the outer terrace.

The outer terrace supports a sparse coral population similar in species composition and morphology to the gorgonian zone. This assemblage is characteristic of the outer slopes of Molasses, French, and Elbow reefs in Key Largo. Large colonies of Montastrea annularis are scattered sporadically over the bottom and, as in the gorgonian zone, support diverse fish populations and frequently, cleaner fish stations. There are small sand channels running seaward and most species of coral are usually small.

Long Key Reef

Long Key Reef lies at the southeastern edge of the Dry Tortugas platform. The study site lies southeast from Fort Jefferson, facing southeast, the direction of the prevailing swell, and away from the direction of most winter storms. The prevailing current pattern over the Tortugas platform is from northwest to southeast such that the water passing over the reef drains from across the entire reef platform (Davis, 1982). This green to blue-green water is laden with organic debris and fine sediment. Estimated horizontal visibility was almost always less than 10 meters during our field session earning the nickname "shadowland" for the reef. The reef supports a large diverse fish population (Jones and Thompson, 1975), along with associated reef algae and gorgonians. Long Key was chosen as the study site as it is the only reef in the Dry Tortugas that displays zonal patterns and geomorphology similar to Carysfort Reef, our primary work site in the northern Keys.

The morphology of Long Key Reef may be seen in Fig. 4, a fathometer tracing which was run over the transect site on a compass heading of 120 degrees magnetic. The reef is backed by a shallow lagoon which leads into a reef flat composed of coral rubble. The seaward edge of the reef flat slopes very gently to a depth of approximately 10 meters where the slope increases. Seaward of the reef are a few scattered gorgonian and coral encrusted rocks. The reef measures just slightly under four hundred meters from the flat to the base of the reef at 18-20m. Long Key Reef (Fig. 5, Table 2.) may be divided into five distinct parallel zones which lie parallel to the

reef flat and tangent to the prevailing seas:

1. Lagoon
2. Reef flat
3. Patch reef zone
4. Gorgonian zone
5. Spur and groove

The lagoon was not surveyed with transects. It consists of small patches of Acropora cervicornis, and Porites porites. There is one small grove of Acropora palmata situated in a channel. This is the only living stand of this species in the area to our knowledge, although the species was much more abundant in the 1800's. In 1976 a cold water thermal shock killed two-thirds of the small stand (Davis, 1982)

The reef flat is composed of loose coral rubble, mostly Acropora cervicornis, Porites spp. and a few Acropora palmata fragments. At high tide it is submerged and is frequently exposed at low tide. The flat appears to be the result of the accumulation of debris tossed up by storms and not the end product of in-situ of coral growth. The gently sloping shallows in front of the flat are sparsely covered with Porites porites, Porites astreoides, Siderastrea radians and support a dense, fleshy algal population. This region stretches approximately fifty meters seaward.

Patch reefs appear when the water depth approaches 5 meters. The algal coverage decreases and the bottom is covered with coarse carbonate sediment, mostly shelly sands and coral fragments. Dotted on this are small rock islands of reef rock that stand 30-50 cm off the bottom. These islands support a dense gorgonian population and about ten species of coral (Photo G). Situated among the reef rock islands are small stands of Acropora cervicornis ranging in size from 0.5-2 meters in diameter. Conspicuously absent are any living colonies of Acropora palmata. An extensive search did turn up a small grove consisting of two or three dead colonies. The encrustation and erosion of their surfaces suggested they died between two and ten years previously. The patch reef region extends for approximately one hundred and thirty meters seaward and ranges in depth from 3-7 meters.

Seaward of the rock islands is an area characterized by soft sediment which supports a very few species of coral at low densities and a luxuriant population of the gorgonian Pseudopterogorgia bipinata (Photo H). This region extends approximately forty to fifty meters.

The coral population becomes more abundant and diverse as the spur and groove region is approached. Species diversity and coverage increase sharply and the reef begins to take on the appearance of a "true" coral reef. The spur and groove region consists of long spurs of coral 2-4 meters in height off the bottom which are 3-15 meters in width and are oriented (120 degrees magnetic) into the prevailing

swell. The principal reef building coral species is Montastrea annularis, which appears in a variety of growth forms from knobby multilobate to large flow sheets of the skirted ecotype (terminology after Dustan, 1975). Colonies approach four meters in diameter and appear to be responsible for the construction of the reef spurs (Photo I). The floors of the grooves are sediment covered with occasional pieces of loose coral rubble. In a few locations bare reef rock was observed in the grooves, probably the result of scouring by the prevailing swell. This region extends for approximately one hundred meters and ends at the base of the reef. It is the most diverse and richly populated region. The colony size of most species reaches a maximum in this region as well.

The internal structure of the spurs between 10 and 18 meters is honeycombed with caves due to the profuse overlapping of coral colonies. In many instances it appears that one large coral colony develops into a mushroom shaped structure creating a cave beneath it. The floors of these caves are covered with fine sediment. The walls are covered with sponges and bryozoans. Fluorescence dye was released into these crevices in an attempt to determine the extent of the labyrinth. Dye released into holes would flow out others 5 to 10m away suggesting that the reef structure is open beneath the veneer of living coral. Large coral colonies of a variety of species appear sporadically along the seaward edge of the escarpment. Such species are Madracis decactis (Photo J), Agaricia lamarcki, Stephanocoenia michelinii, Montastrea cavernosa, and Montastrea annularis. Of these, only Montastrea annularis is commonly larger than a meter in diameter in other habitats on the reef.

Discussion of Carysfort Reef

Carysfort Reef marks the northern extent of lush populations of reef-building corals along the eastern coast of North America. Mayor (1914) suggested that reduced water temperature further north limited the northern extent of reef development. South of Key Largo reef development may be limited by tidal passes that allow water from Florida Bay to flow onto the shelf platform on the ebb tide (Ginsburg and Shinn 1964) or, conversely, allow cool subsurface water from the Straits of Florida to intrude into the shallows of the shelf platform (Dustan, et al., 1976). Thus Carysfort appears to be situated at or just south of the thermal tolerance point of active reef development and paradoxically, is one of the most well developed reefs in the entire Florida Keys.

The vertical distributions of coral coverage and number of species are almost independent of each other on the reef flat and in the shallows. Coral coverage and the number of species become more closely correlated in deeper water (Fig.3). Maximal species number occurs at the outer edges of the terraces, seaward of maximal coral coverage, hinting that spatial competition in these areas may be intense, or that subtle environmental differences between a terrace and break in slope may reorder community structure (Porter, 1972).

Substrate heterogeneity at the edge of a break in slope, or water circulation enhancement may create a more favorable environment for larval settlement as well. In any case, it must be remembered that reef growth, with the exception of the reef flat, is proceeding upwards so that today's edge is part of tomorrow's terrace. As such the species composition of the reef may be influenced by the morphology of the reef which, in turn, affects the future species composition. Active reef growth in shallow water on Carysfort is a function of the growth of Acropora palmata and Millepora complanata. The seaward geomorphology of the reef flat and the spur and groove formations are formed mostly by Acropora palmata as first described for Key Largo Dry Rocks by Shinn (1963). Deeper, it appears that Montastrea annularis and other massive corals contribute to the growth of the reef frame.

The species composition of the gorgonian zone on Carysfort is similar to the outer reef slopes of other reefs in the northern Keys: Molasses, Elbow, French Reefs. On these reefs the gorgonian population gradually decreases as water depth increases towards the Straits of Florida. On Carysfort, however, this zone ends abruptly at 10 meters where it is replaced by a diverse coral community. The appearance of a rich coral community and the disappearance of the rich gorgonian community at 10m occurs as a sharp line and is very apparent even to a casual visitor to the reef. This suggests that some environmental parameter change sharply at this depth, strongly influencing reef community development (Photo D).

Waves heading into Carysfort Reef first meet with the outer terrace some 300 meters seaward of the reef (Fig. 2). The shallowest depth of the platform is 10 meters so that wave energy below 10 meters is attenuated. The outer terrace thus shields the fore-reef terrace population from the full force of the prevailing swells and storm seas that pound the other outer reefs. We have witnessed this sheltering phenomena while diving on Carysfort during seas of 1-2 meter wave height. At depths below 10 meters the surge is greatly reduced and occurs as a sharp boundary just at the beginning of the fore reef coral population. In the winter and spring months we have observed sharp discontinuities in temperature and underwater visibility between 10 meters and the top of the escarpment at 15 meters. Whenever these differences in water masses have been observed warmer, clearer water overlays cooler, more turbid water. Either the cold water is intruding into the surface waters along the edge of the Gulf Stream as noted in the Dry Tortugas (Dustan et. al., 1976) or cooler water from the back reef area is becoming trapped in the moat region between the inner and outer platform of Carysfort. The reduction of wave action results in finer sediments on the fore-reef slope and escarpment at Carysfort than on neighboring reefs. Sediments from these zones on Carysfort have sponge boring chips, spicules and fine sedimentary particles in great abundance. The sediments at comparable depths on Molasses Reef consist of much coarser carbonate particles. It is conceivable that the moat region of Carysfort serves as a sink for the deposition of fine sediment and

therefore may contain a detailed record of the depositional history of the northern Florida Keys.

Discussion of Long Key Reef

The species zonation on Long Key Reef follows the classical pattern first described for West Indian coral reefs (Goreau, 1959), but there are some distinct differences. Most conspicuous of these are the absence of Acropora palmata and an associated reef flat community. The reef flat appears to be formed by the accumulation of coral skeleton rubble rather than infilled, cemented Acropora palmata skeletons in growth position as seen at Carysfort and so characteristic of other Florida Keys Reefs (Shinn, 1963, 1977). Seaward of the reef flat where one would expect to find groves of A. palmata the substrate is covered mostly with algae and gorgonians, and a few scattered corals. Observations along the edge of the reef flat subsequently turned up a stand of dead A. palmata (in addition to the one known living stand mentioned earlier) in growth position suggesting that while this species may inhabit the zone it suffers high mortality and never reaches the population densities found elsewhere in the Florida Keys. Reports of a massive coral mortality as a result of "black water" are mentioned in the first Carnegie Reports of the Dry Tortugas (Mayer, 1902), and in 1977 a cold water (13 degrees C) intrusion resulted in the death of almost all the Acropora cervicornis on the platform (Davis, per. comm). Thus periodic climatic fluctuations, possibly combined with severe storms, may prevent Acropora palmata from establishing itself as a major reef-building species in the sediment laden water of the Dry Tortugas.

Along with the noted absence of Acropora palmata is the absence of a Millepora-gorgonian species association commonly seen in the Keys and Bahamas. Both species occur in the Dry Tortugas but do not form the assemblage so common elsewhere. The assemblage is commonly found on the tops of shallow reef flat spurs constructed by Acropora palmata. Possibly the absence of Acropora palmata and the habitat its structure creates results in the deletion of the Millepora-gorgonian species complex. Conversely, the lack of a similar necessary ecological condition (high surf, clear water, favorable temperature) may be the controlling factor in the distribution of both assemblages.

Coral coverage is closely correlated with species number on Long Key Reef (Fig. 5). The absence of high coverage in shallow water is attributed to an absence of Acropora palmata and its associated Millepora-gorgonian species complex. Coverage is highest deeper than 10m where the most active reef accretion appears to be occurring.

CONCLUSIONS

The species composition and zonation patterns of a coral reef are the result of species' differential abilities to settle, adapt, and survive the prevailing environmental conditions. The environmental parameters of light, water temperature and wave action, sedimentation, and food availability all have been thought to be of primary importance to corals. Biological interactions between and among species operate at organizational levels within this adaptive framework (Porter, 1974; Glynn, 1976; Connell, 1978). The interplay of biological and physical factors result in higher order interactions that determine community structure (Futuyma, 1979). Coral communities at both study sites show a positive correlation between average colony size and percentage cover. On Long Key Reef increases in coral coverage are the result of all species becoming more abundant. On Carysfort Reef increases in cover are sometimes the result of single species dominance, as in the Acropora palmata zone, or a general increase in all species as seen on the fore-reef terrace.

The differences in patterns suggest that different environmental and biological pressures control the development of these two reef communities. Part of the reason for the differences in these two reefs may lie in their positions relative to the path of the Gulf Stream. Carysfort Reef lies at the edge of the Gulf Stream and is often bathed in its waters, while the Dry Tortugas are approximately 10-20 miles north of the edge of the Gulf Stream and only occasionally experience clear oceanic water. The prevailing patterns of water movement over the Dry Tortugas result in a northwest to southeast flow so that the water passing over Long Key Reef has drained from the Dry Tortugas Platform. Thus there appears to be major differences in the quality of the water over the two reefs. In addition, the Gulf Stream buffers the population at Carysfort against cold water intrusions in the winter so that even though it is much farther north than Long Key, the minimum water temperatures are somewhat higher. There are reports (Mayer, 1914) of elevated water temperatures occurring in the Dry Tortugas in the summer coincident with periods of calm and low spring tides which resulted in the death of corals. Temperatures in shallow parts of the reef ranged from 33-38 degrees C. On Carysfort Reef this type of localized water heating seems unlikely as the reef is situated far from any other large geomorphic structures and the water is kept moving longshore by the Gulf Stream.

Both reefs (Long Key and Carysfort) face into the direction of the prevailing winds and swell. However, Carysfort does not receive the full force of the swell at depths below 10 meters as the fore-reef terrace is protected by the second platform seaward of it. This platform blocks the deeper swell and may help to explain the absence of well defined surge channels on Carysfort Reef. Observations on the species composition of the seaward slope of the outer platform have shown it to be similar to the outer slopes of neighboring reefs that

are not protected from the swell. These regions are sparsely covered by coral and give the appearance of being "wave battered". The rich and diverse coral population on the fore-reef terrace of Carysfort Reef below 10 meters is not typical of other reefs in the Keys. Whether or not this atypical species assemblage is the direct result of a decrease in wave shock, change in food supply or sediment composition, or some other factor cannot be determined at this time; but remains as an intriguing question to be attacked at a future date.

One of the initial objectives of this research was to study differences between the two reefs in an attempt to dissect out the impact of man on Carysfort Reef. However, upon completion of the Long Key Reef survey it became apparent that the two reefs are very different in structure and form as a result of a suite of different environment parameters. There are some general observations that deserve comment however, and though they have not been quantified, they may be instructive as to the mechanisms behind man's impact on coral reefs.

The incidence of broken coral colonies is high on Carysfort Reef. Broken colonies must expend metabolic energy to their wounds and regrow skeleton lost to damage. It is hard to single out the greatest cause of physical damage to reefs by man but it is fair to say that constantly occurring damage as a result of anchoring, diving, and fishing is slowly but surely decreasing the amount of framework carbonate that corals add to the reef structures of the northern keys, and it is apparent on Carysfort Reef. Commensurate with these observations is the high incidence of corals with broken or damaged tissue as a result of excess sedimentation, algal overgrowth and algal disease (Dustan, 1977). Again, such mortality factors were occasionally seen in the Dry Tortugas, most notable is the havoc caused by anchoring in the lee of Loggerhead Key (Photo K, Davis, 1977).

The comparison presented in this study has provided an initial look at the community structure of two reefs at the opposite ends of the Florida Keys. Differences in community structure appear to be the result of local environmental differences and local geomorphological features. Severe periodic environmental perturbations may control the distribution of less tolerant species (Acropora palmata and Acropora cervicornis) in the Dry Tortugas. The Gulf Stream may reduce the probability of similar perturbations occurring on Carysfort Reef. Both reefs may be exposed to storms which may also affect their species composition and geomorphology. Resurveys of these communities in the future will begin to reveal their temporal as well as spatial variability.

References

- Adey, W.H. (1975) Algal ridges and coral reefs of St. Croix, their structure and Holocene development. *Atoll Res. Bull.* 187:1-66
- Connell, J.H. (1978), Diversity in tropical rain forests and coral reefs, *Science* 199(4335), 1302-1310.
- Davis, G.E. (1977), Anchor damage to a coral reef on the coast of Florida, *Biol. Conserv.* 11:29-34.
- Dustan, P. (1975), Genecological differentiation in the reef-building coral Montastrea annularis, Ph.D. thesis, State University of New York at Stony Brook.
- Dustan, P. (1975a), Growth and form in the reef-building coral Montastrea annularis, *Marine Biology* 33:101-107.
- Dustan, P., W. Japp and J. Halas (1976), Notes on the distribution of members of the Class Sclerospongiae, *Lethaia* 9(4), 419-420.
- Dustan, P. (1977), Vitality of reef coral populations off Key Largo, Florida: recruitment and mortality, *Environmental Geology* 2:51-58.
- Futuyma, D. (1979), Evolutionary Biology, Sinaur Associates (Sunderland, Mass.), 565 pp.
- Ginsburg, R.N. and E.A. Shinn (1964), Distribution of the reef-building community in Florida and the Bahamas (abs), *Amer. Assoc. Pet. Geol. Bull.* 48:527.
- Glynn, P.W. (1976), Some physical and biological determinants of coral community structure in the Eastern Pacific, *Ecol. Monographs* 46(4), pp. 431-456.
- Goreau, T.F. (1959), The ecology of Jamaican coral reefs I, species composition and zonation, *Ecology* 40:67-90.
- Goreau, T.F. and J.W. Wells (1967), The shallow-water Scleractinia of Jamaica: revised list of species and their vertical distribution range, *Bull. Mar. Sci.* 17:442-453.
- Hodges, L.T. 1977. Coral size and orientation relationships of the Key Largo limestone, Florida. *Proc. 3rd Int. Coral Reef Symp.* (Univ. Miami, Fl). pp.348-352
- Hoffmeister, J.E. and H.G. Multer (1964), Geology and origin of the Florida Keys, *Geol. Soc. Amer. Bull.* 75: 1487-1502.

- Jones, R.S. and M. J. Thompson (1978), Comparison of Florida reef fish assemblages using a rapid visual technique, *Bull. Mar. Sci.* 28(1): 159-172.
- Kinzie, R.A.K. III (1973), The zonation of West Indian gorgonians, *Bull. Mar. Sci.* 23:93-155.
- Loya, Y. (1972), Community structure and species diversity of hermatypic corals at Eilat, Red Sea, *Mar. Biol.* 13:100-123.
- Mayer, A.G. (1902). The Tortugas, Florida as a station for research biology. *Science* 17:190-192
- Mayor, A.G. (1914), The Effects of Temperature on Tropical Marine Animals, Carnegie Institute, Washington, Pub. 183, 6:1-24,
- Porter, J.W. (1972), Patterns of species diversity in Caribbean reef corals, *Ecology* 53:745-48.
- Porter, J.W. (1974), Community structure of Coral Reefs on Opposite Sides of the Isthmus of Panama, *Science* 186:543-545.
- Shinn, E.A. (1963), Spur and groove formation on the Florida Reef Tract. *Jour. Sed. Pet.* 33,2: 291-303.
- Shinn, E.A. (1980), Geologic history of Grecian Rocks, Key Largo Coral Reef Marine Sanctuary. *Bull. Mar. Sci.* 30,3: 646-656.
- Shinn, E.A., J.H.Hudson,R.B.Halley, and B. Lidz (1977), Topographic control and accumulation rate of some Holocene coral reefs: South Florida and Dry Tortugas. *Proc. 3rd Int. Coral Reef Symp.* Vol 2: Geology. (Univ. Miami, Fl.) pp.1-7
- Storr, J.F. (1964), Ecology and Oceanography of the Coral-Reef Tract, Abaco Island, Bahamas. *GSA Special Papers* No. 79.

Table 1: Coral species coverage on different morphological zones
Carysfort Reef, Key Largo

Species	Mean Percent Coverage by Zone						
	RF	A.pal	Trough	Ridge	GZ	FRT	FRE
<i>Acropora palmata</i>	0	36.2	9.0	0	0	0	0
<i>Acropora cervicornis</i> . .	0	0	3.6	0	0	30.4	0
<i>Mycetophyllia lamarckana</i>	0	0	0	0	0.2	<1	<1
<i>Mycetophyllia ferox</i> . .	0	0	0	0	0.2	1.6	<1
<i>Mycetophyllia danana</i> . .	-	-	-	-	-	-	-
<i>Mycetophyllia aliciae</i> . .	0	0	0	0	0	0	<1
<i>Solenastrea hyades</i> . . .	0	0	0	0	0	0	1.2
<i>Agaricia agaricites</i> . . .	<1	1.0	1.7	2.9	<1	<1	1.0
<i>Agaricia lamarcki</i> . . .	0	0	0	0	0	<1	0
<i>Agaricia fragilis</i> . . .	0	0	0	0	0	<1	0
<i>Helioseris cucullata</i> . .	0	0	<1	<1	0	<1	0
<i>Colpophyllia natans</i> . . .	0	0	0	0	0	2.2	<1
<i>C. breviserialis</i>	0	0	0	0	0	7.6	<1
<i>Scolymia cubensis</i> . . .	0	0	0	0	0	<1	<1
<i>Scolymia lacera</i>	-	-	-	-	-	-	-
<i>Mussa angulosa</i>	-	-	-	-	-	-	-
<i>Montastrea annularis</i> . .	<1	0	0	0	<1	17.5	1.7
<i>Montastrea cavernosa</i> . .	0	0	0	1.1	0	<1	1.1
<i>Manicina areolata</i> . . .	-	-	-	-	-	-	-
<i>Favia fragum</i>	0	<1	<1	0	<1	0	0
<i>Siderastrea radians</i> . . .	0	0	0	0	<1	0	0
<i>Siderastrea sidera</i> . . .	0	<1	<1	0	<1	3.3	6.8
<i>Dichocoenia stokesii</i> . .	0	0	0	0	<1	<1	0
<i>Stephanocoenia michelinii</i>	0	0	0	0	<1	1.5	2.2
<i>Diploria strigosa</i>	-	-	-	-	-	-	-
<i>Diploria clivosa</i>	-	-	-	-	-	-	-
<i>Diploria labyrinthiformis</i>	-	-	-	-	-	-	-
<i>Isophyllia sinuosa</i> . . .	-	-	-	-	-	-	-
<i>Isophyllastrea rigida</i> . .	-	-	-	-	-	-	-
<i>Porites porites</i>	<1	0	0	0	<1	<1	<1
<i>Porites astreoides</i> . . .	3.7	1.5	3.4	4.2	<1	<1	1
<i>Porites furcata</i>	0	0	0	0	0	<1	0
<i>Madracis</i> spp.	0	0	0	0	0	<1	0
<i>Madracis decactis</i> . . .	0	0	0	0	0	<1	<1
<i>Millepora alcicornis</i> . . .	0	0	<1	0	<1	<1	0
<i>Millepora complanata</i> . .	3.4	7.2	10.5	48.0	0	7.0	<1
<i>Eusmilia fastigiata</i> . . .	0	0	0	0	0	<1	<1
Number of species in each zone	6	7	9	5	11	24	17
Number of transects . . .	4	3	3	1	2	5	3
Distance along transect from base of reef (m)	320- 260	250- 230	200- 160	140	100- 120	80- 40	30- 0

Note: RF=back reef + reef flat , A.pal= *Acropora palmata* zone,
GZ= gorgonian zone, FRT=fore-reef terrace, FRE= fore reef escarpment,
Dash signifies presence on Long Key but absent on Carysfort Reef.

Table 2: Coral species coverage on different morphological zones
Long Key Reef, Dry Tortugas

Species	Mean Percent Coverage by Zone				
	Patch Reefs	Gorgonian	Spur 1	and Groove 2	3
<i>Acropora palmata</i>	-	-	-	-	-
<i>Acropora cervicornis</i>	<1	<1	<1	4.6	0
<i>Mycetophyllia lamarckana</i>	0	0	<1	<1	<1
<i>Mycetophyllia ferox</i>	0	0	0	2.2	<1
<i>Mycetophyllia danana</i>	0	0	0	<1	0
<i>Mycetophyllia aliciae</i>	0	0	0	<1	0
<i>Solenastrea hyades</i>	-	-	-	-	-
<i>Agaricia agaricites</i>	<.5	<.5	<1	1	<1
<i>Agaricia lamarcki</i>	0	0	0	0	5.2
<i>Agaricia fragilis</i>	0	0	0	<1	<1
<i>Helioseris cucullata</i>	0	0	0	<1	<1
<i>Colpophyllia natans</i>	0	0	<1	2	<1
<i>C. breviserialis</i>	0	0	0	<1	0
<i>Scolymia cubensis</i>	0	0	0	0	<1
<i>Scolymia lacera</i>	0	0	0	0	<1
<i>Mussa angulosa</i>	0	0	0	<1	0
<i>Montastrea annularis</i>	0	0	<1	15.0	10.3
<i>Montastrea cavernosa</i>	0	<1	<1	4.6	6.8
<i>Manicina areolata</i>	0	0	<1	0	0
<i>Favia fragum</i>	-	-	-	-	-
<i>Siderastrea radians</i>	<.5	0	0	0	0
<i>Siderastrea sidera</i>	<.5	<.5	4.5	4.8	7.5
<i>Dichocoenia stokesii</i>	0	<.5	<1	0	0
<i>Stephanocoenia michelinii</i>	0	0	<1	1.2	3.0
<i>Diploria strigosa</i>	0	<.5	0	0	0
<i>Diploria clivosa</i>1.5	<1	0	<.5	0
<i>Diploria labyrinthiformis</i>	0	<1	<.5	<1	0
<i>Isophyllia sinuosa</i>	0	<.5	<.5	<.5	0
<i>Isophyllastraea rigida</i>	<.5	0	0	<.5	0
<i>Porites porites</i>	<.5	1.2	9	1	<1
<i>Porites astreoides</i>	<1	1.1	1	2.1	1
<i>Porites furcata</i>	-	-	-	-	-
<i>Madracis</i> spp.	-	-	-	-	-
<i>Madracis decactis</i>	0	0	0	<1	<1
<i>Millepora alcicornis</i>	<.5	<1	<1	<1	<1
<i>Millepora complanata</i>	-	-	-	-	-
<i>Eusmilia fastigiata</i>	0	0	<.5	<.5	0
Number of species in each zone	9	12	16	24	17
Number of transects	4	8	6	5	5
Distance along transect from base of reef (m)	370- 300	290- 180	160- 110	100- 50	40- 0

Note: Dash (-) signifies presence on Carysfort but absent on Long Key

Table 3. Species List for Areas of Study

Species	Dry Tortugas	Long Key Reef	Key Largo	Carysfort Reef
Acropora palmata	*	—	*	*
Acropora cervicornis	*	*	*	*
Mycetophyllia lamarckana	*	*	*	*
Mycetophyllia ferox	*	*	*	*
Mycetophyllia danana	*	*	*	*
Mycetophyllia aliciae	*	*	*	*
Solenastrea hyades	*	*	*	*1
Agaricia agaricites	*	*	*	*
Agaricia lamarcki	*	*	*	*
Agaricia fragilis	*	*	*	*
Helioseris cucullata	*	*	*	*
Colpophyllia natans	*	*	*	*
Colpophyllia breviserialis	*	*	*	*
Scolymia cubensis	*	*	*	*
Scolymia lacera	*	*	*	*
Mussa angulosa	*	*	*	*
Montastrea annularis	*	*	*	*
Montastrea cavernosa	*	*	*	*
Dendrogyra cylindrus	—	—	*	—
Manicina areolata	*	*	*	*
Favia fragum	*	*	*	*
Favia conferta	*	—	—	—
Siderastrea radians	*	*	*	*
Siderastrea sidera	*	*	*	*
Dichocoenia stokesii	*	*	*	*
Dichocoenia stellaris	*	*	*	*
Stephanocoenia michelinii	*	*	*	*
Diploria strigosa	*	—	*	—
Diploria clivosa	—	—	*	*
Diploria labyrinthiformis	*	—	*	*
Isophyllia sinuosa	*	*	*	*
Isophyllastraea rigida	*	*	*	—
Porites porites	*	*	*	*
Porites astreoides	*	*	*	*
Porites furcata	—	—	*	*
Madracis spp.	*	*	*	*
Madracis decactis	*	*	*	*
Millipora alcicornis	*	*	*	*
Millipora complanata	*	—	*	*
Eusmilia fastigiata	*	*	*	*
Oculina diffusa	*	*	*	—
Cladocora spp.	*	—	—	—
Meandrina meandrites	*	*	*	*

* = present, — = absent

1: outer terrace only

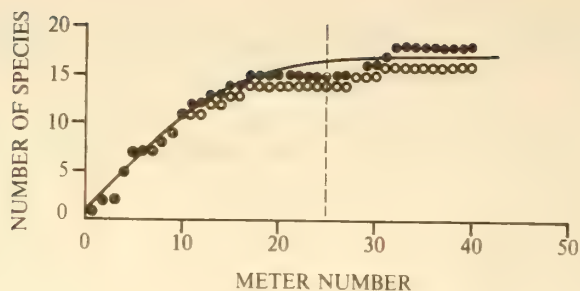


Fig. 1. Species-area curve for reef coral species on Carysfort Reef, Key Largo, Florida. Transects were run at a depth of 17 meters on the fore-reef terrace of the study site.

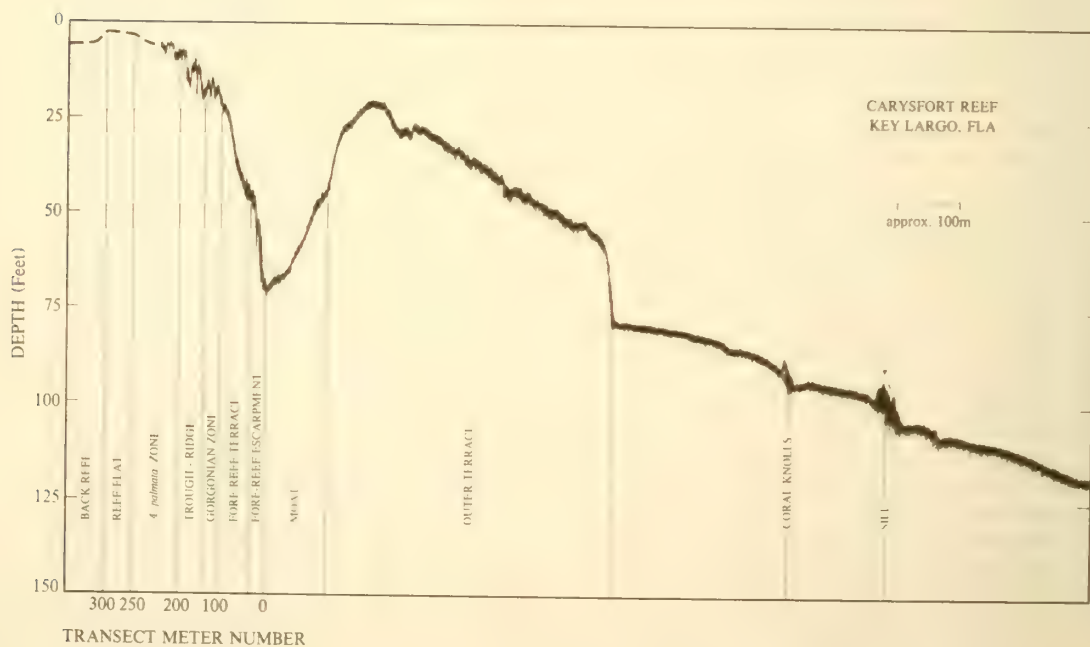


Fig. 2. Fathometer tracing of Carysfort Reef showing the overall morphology of the reef. Note the terrace seaward of the study site which rises to a depth of 10 meters.

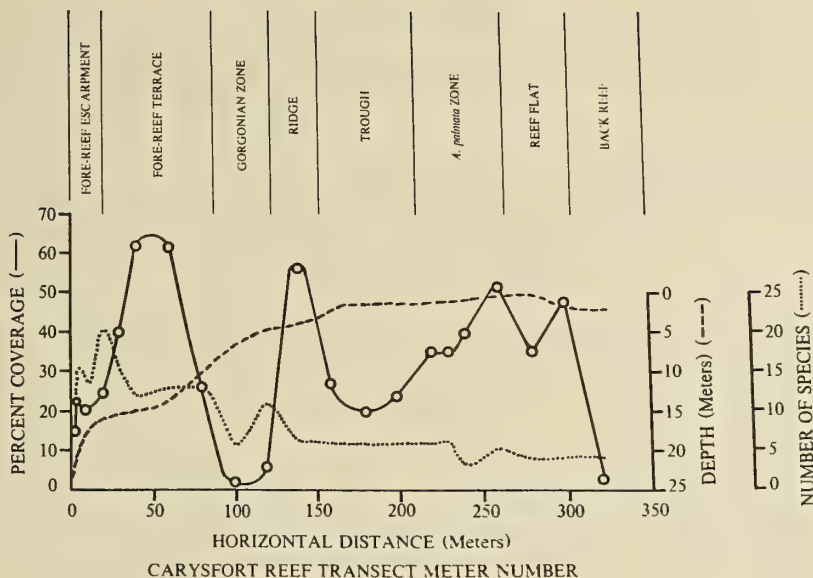


Fig. 3. Graph depicting the percentage coral cover, number of species, and depth profile of Carysfort Reef study site.

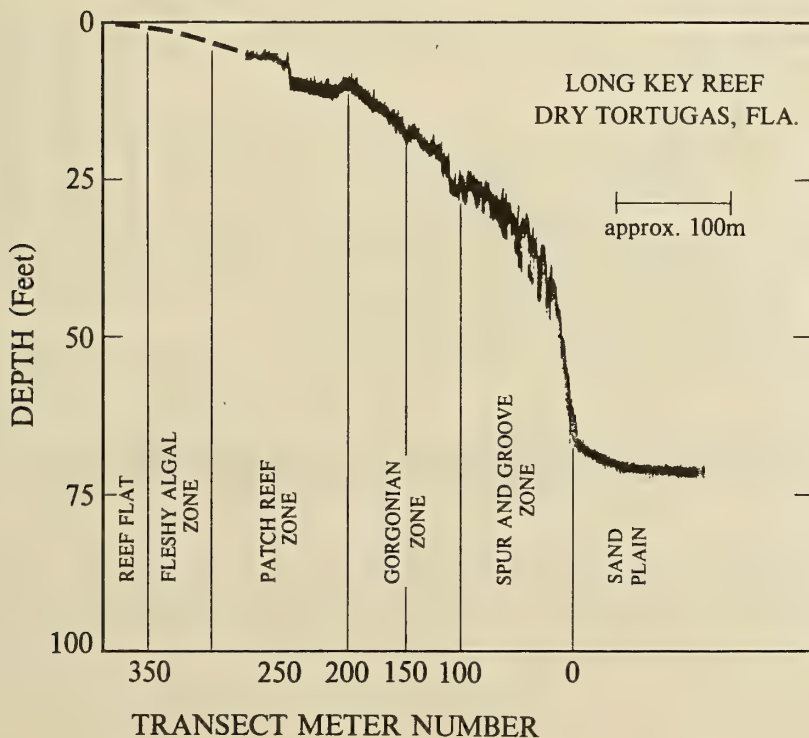


Fig. 4. Fathometer tracing of Long Key Reef, Dry Tortugas showing the overall morphology of the reef. Note the absence of an offshore terrace.

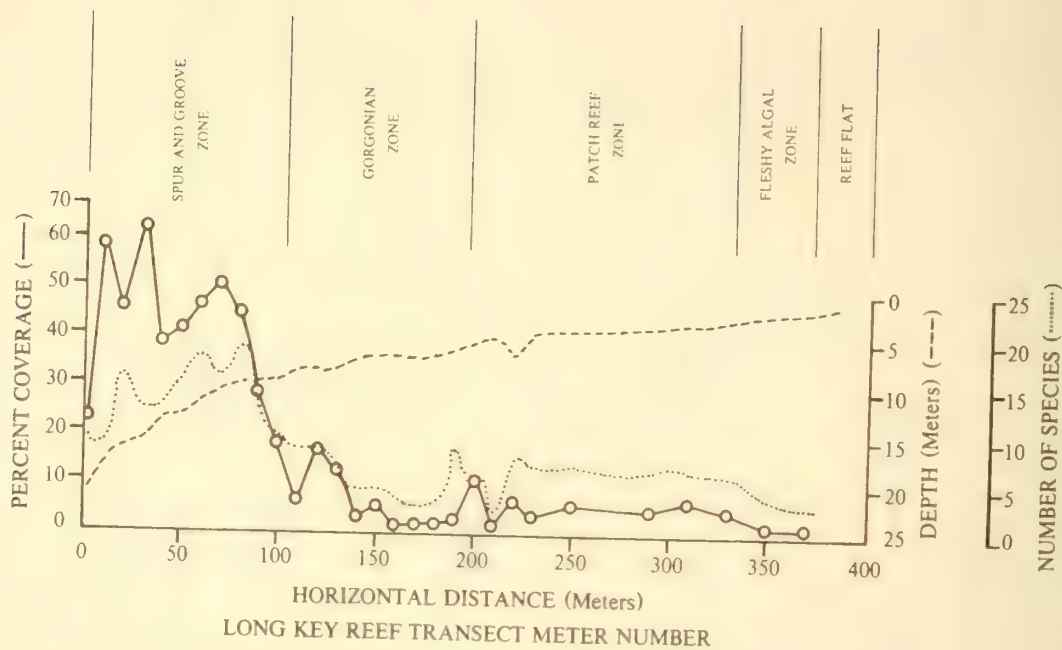


Fig. 5. Graph depicting the percentage coral cover, number of species, and depth profile of Long Key Reef study site.

Photograph Legends

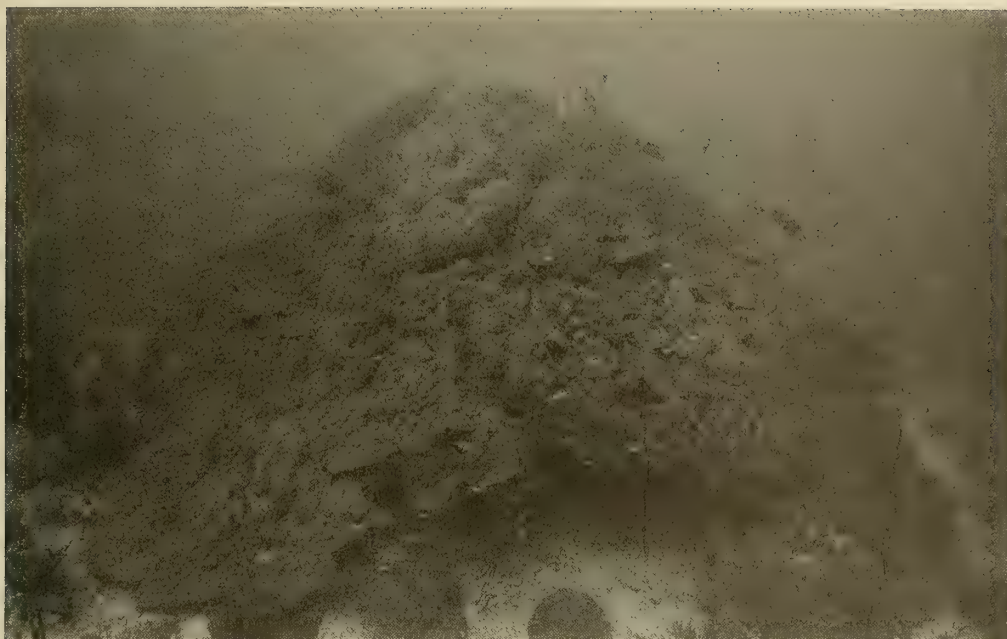
- A. Dense thickets of *Acropora palmata* on the seaward edge of the reef flat of Carysfort Reef.
- B. A rich gorgonian, sponge and algal community inhabits the gorgonian zone on the fore-reef terrace from about 5m to 10m. Scleractinian corals such as P. Porites (2) and D. stokesii (1) comprise less than 10% of the total coverage. The colony of D. stokesii is approximately 12cm in diameter.
- C. Large colonies of *M. annularis* occur sporadically in the gorgonian zone of Carysfort reef. Such colonies act as islands on the plain and become centers of focus for fish and invertebrate populations. This colony is approximately 3m high and 6.4m in greatest diameter.
- D. The ecotone between the gorgonian zone (right) and the fore-reef slope (left) is extremely sharp (arrows). Coral coverage changes from less than 10% to greater than 25% in less than 3 meters horizontal distance at a depth of 10m on Carysfort Reef.
- E. A large spreading colony of *Agaricia* spp. is covering a large block of reef rock, apparently a talus block from an earlier slump.
- F. View of the escarpment of Carysfort Reef, 18m. Virtually every colony in the view is surrounded by fine sediment which collects on the escarpment as a result of wave attenuation by the outer reef platform.
- G. A reef rock island on the fore-reef terrace of Long Key Reef. This particular island has been formed by M. annularis and M. alcicornis. 5m
- H. Luxuriant population of P. bipenata inhabits a 50m wide zone on Long Key Reef at a depth of 4-6 meters. The largest of these colonies are 1.5 to 2m in height.
- I. A narrow sand channel slowly being overgrown by a large colony of M. annularis illustrates the hollowness of the spur and groove zone on Long Key Reef. 12m.
- J. Diver Karen Lukas examining an exceptionally large colony of M. mirabilis at the base of Long Key Reef, 18m.
- K. An anchor, probably lost by a fishing boat, embedded in a patch of A. cervicornis on Long Key Reef. Note the broken and dead rubble surrounding the shank. The coral is regenerating and will eventually overgrow the anchor, 10m.



A. Dense thickets of *Acropora palmata* on the seaward edge of the reef flat of Carysfort Reef.



B. A rich gorgonian, sponge and algal community inhabits the gorgonian zone on the fore-reef terrace from about 5m to 10m. Scleractinian corals such as P. Porites (2) and D. stokesii (1) comprise less than 10% of the total coverage. The colony of D. stokesii is approximately 12cm in diameter.



C. Large colonies of *M. annularis* occur sporadically in the gorgonian zone of Carysfort reef. Such colonies act as islands on the plain and become centers of focus for fish and invertebrate populations. This colony is approximately 3m high and 6.4m in greatest diameter.



D. The ecotone between the gorgonian zone (right) and the fore-reef slope (left) is extremely sharp (arrows). Coral coverage changes from less than 10% to greater than 25% in less than 3 meters horizontal distance at a depth of 10m on Carysfort Reef.



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F. View of the escarpment of Carysfort Reef, 18m. Virtually every colony in the view is surrounded by fine sediment which collects on the escarpment as a result of wave attenuation by the outer reef platform.



G. A reef rock island on the fore-reef terrace of Long Key Reef. This particular island has been formed by M. annularis and M. alcicornis. 5m



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ATOLL RESEARCH BULLETIN

No. 289

THE DISTRIBUTION, ABUNDANCE AND PRIMARY PRODUCTIVITY
OF SUBMERGED MACROPHYTES IN A BELIZE BARRIER-REEF
MANGROVE SYSTEM

By

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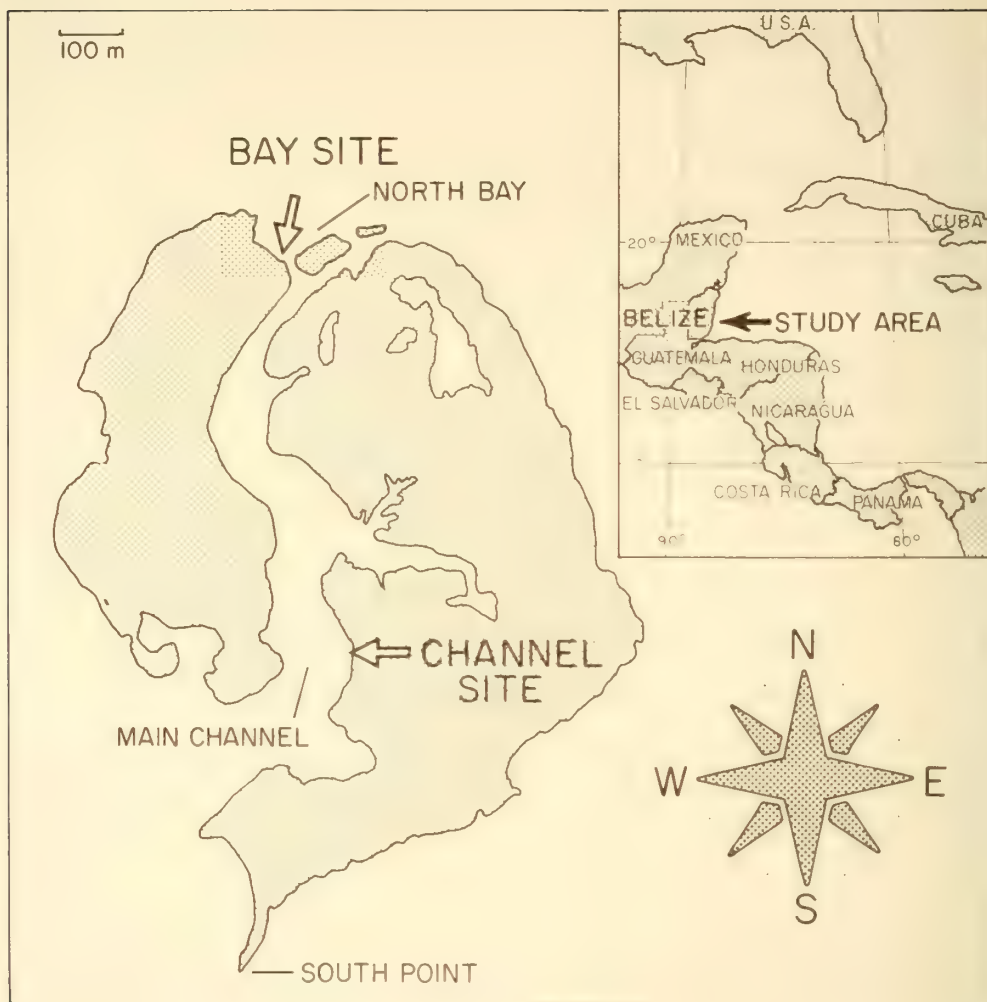


Figure 1. Location of Twin Cays study sites on the Belize barrier reef.

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ABSTRACT

The comparison of wave-exposed (bay) to sheltered (channel) macrophyte assemblages in a Belize mangrove system revealed higher standing stocks of productive filamentous algae in the latter, correlated with relatively low levels of physical disturbance from sea urchin herbivory and wave turbulence. The sheltered channel site, while containing fewer total species and lower species richness, exceeded the bay site in total cover and species evenness. The Shannon-Weaver index of diversity was nearly equal at both sites. Five species comprised 96% of the cover at the bay site, led by the jointed calcareous alga Halimeda opuntia f. triloba (37%) and Thalassia testudinum (26%); whereas, H. opuntia f. triloba (40%), Amphiroa fragilissima (22%) and T. testudinum (16%) provided the majority of the total community productivity. At the channel site, six taxa contributed 96% of the cover, dominated by a mat-forming, gelatinous, filamentous species of naviculoid diatom (29%) and Caulerpa verticillata (28%). Major primary producers at the channel site were the three cover dominants, the gelatinous diatom (24% of the total community carbon fixed), C. verticillata (22%) and H. opuntia f. triloba (20%). The total daylight community primary productivities at the two sites (bay = 17.2, channel = 13.4 grams carbon fixed per meter squared of substratum per day ranked among the higher rates recorded for dense seagrass beds and were considerably higher than those reported for most calcareous reef flat habitats. This high apparent photosynthetic potential may be related to reduced levels of herbivory and a greater availability of recycled nutrients near mangrove islands.

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INTRODUCTION

The fringing-reef margins of tropical atolls and coastal zones represent shallow subtidal to intertidal calcareous frameworks with diverse epibiota that have received intensive study in recent years. Diverse algal standing stocks have been described for Curacao, Dutch West Indies (e.g. Van Den Hoek et al. 1975) and Saint Croix, U.S. Virgin Islands (Connor and Adey 1977) in the Caribbean. Pacific reefs, such as Enewetak Atoll, U.S. Trust Territory (Odum and Odum 1955); Waikiki reef, Hawaii (Doty 1971; Littler 1973a); Guam, U.S. Trust Territory (Tsuda 1971); American Samoa (Dahl 1972); Kaneohe Bay, Hawaii (Smith 1973); and Heron Island, Australia (Hatcher 1982; Hatcher and Larkum 1983), have been the subjects of comparable studies.

While mangrove communities coincide with the worldwide distributions of calcareous biotic reefs and dominate many of the world's tropical and subtropical coastal zones, relatively little work has been done on the standing stocks of benthic macrophytes on the flats that border mangrove islands. On mangrove islands, like coral islands, organisms comprise the major structural elements, but unlike most biotic reef communities, mangrove islands are intertidal, endure wider fluctuations in temperature and salinity and tend to contain silty submerged substrata. Because of their interesting characteristics and a paucity of background information, we initiated a quantitative survey of mangrove macrophyte distributions, abundances and productivities as a necessary basis for the design of further, more specialized experimental studies (e.g. Taylor, Littler and Littler, submitted).

A classification of marine plant functional-form groups [see Littler, Littler and Taylor (1983) for definitions] has been used to interpret (1) productivity patterns over broad geographic areas (Littler and Arnold 1982), (2) evolutionary changes with respect to fluctuations in herbivory through geological time (Steneck and Watling 1982), (3) holistic views of tropical barrier-reef seaweed ecology (Littler, Littler and Taylor 1983), (4) biogeographical responses of algae to herbivory (Gaines and Lubchenco 1982) and (5) the effects of disturbance on subtropical (Littler and Littler 1984) and temperate (Murray and Littler 1984) macrophyte communities. The functional-group approach is an effective mechanism for assessing complex community patterns without having to tediously deal with the demography of each of the component species. Consequently, we felt it would be instructive to analyze the Twin Cays macrophyte populations from this framework.

METHODS AND MATERIALS

Study Areas

Twin Cays is a mangrove system (16°50'N, 80°06'W) representative of similar pristine offshore islands within the lagoonal portion of the Belize barrier system. The island (Fig. 1; see also Rützler and Macintyre 1982) is divided by a main channel that grades toward each opening into shallow beds of Thalassia testudinum Banks ex Kuhnig.

After extensive reconnaissance of the Twin Cays shoreline, the precise location of the upper end of each study transect was determined (by consensus of several experienced marine ecologists) along biologically representative portions of two major benthic habitat types. The channel study site, located on the east side of the main channel, is protected from wave action, with only moderate tidal currents controlling water exchange. The area studied is a typical subtidal mud bank extending 5.5 m outward to a dropoff from intertidal Rhizophora mangle Linnaeus into the meandering 0.5 to 4.0 m deep main channel dominated by Thalassia and Caulerpales. In contrast, the less-sheltered bay site on the northern margin of the island (Fig. 1) typifies habitats where waves and currents are greater, frequently resulting in the mud banks being partially eroded to form vertical walls or undercut ledges. The mud bank studied is 6.5 m wide and terminates abruptly where an undercut bank extends down to a 3.0 m deep silt substratum with sparsely scattered plants of the algal genus Caulerpa [C. mexicana (Sonder) Kützling and C. sertularioides (Gmelin) Howe].

Transects

Data were obtained on 11-12 April 1980 by photographing numbered quadrats perpendicular to the substratum with a 35 mm Nikonos camera equipped with an electronic flash unit and using Kodachrome 64 transparency film. Each quadrat contained a plastic label affixed to the upper left corner that was marked with a wax pencil to identify permanently each of the photosamples.

In the laboratory, the developed transparencies were projected onto a sheet (21 x 28 cm) of white bristol paper. The paper contained a grid pattern of dots at 2.0 cm intervals on the side of the transmitted light; this has been shown (Littler and Murray, 1975) to be an appropriate density (i.e. 1.0 per cm²) for consistently reproducible estimates of cover. The number of dots superimposed on each species was then scored twice (i.e. replicated after movement of the grid) with the percentage cover values expressed as the number of "hits" for each species divided by the total number of dots contained in the quadrats. Reproducibility was high and seldom varied more than $\pm 5\%$ for a given species. Species that were not abundant enough to be scored by the replicated grid of point intercepts were assigned a cover value of 0.1%. In cases of multi-layered communities, more than one photograph per quadrat was taken to quantify each stratum after upper strata had successively been moved aside, often yielding total biotic coverages of greater than 100%.

The method as applied here does not allow for the quantification of microalgae (small epiflora or inflora) when they occur in low abundances. We realize that these may be metabolically very active, but their analysis requires special techniques and expertise, which comprise separate problems in themselves. For this reason, our measurements were restricted to macrophytes that could be discerned in the field with the unaided eye. However, we did quantify microflora (e.g. mats of a filamentous diatom) when it occurred in high abundances. Twenty three contiguous quadrats along a 6.65 m transect were taken at the bay site while 31 quadrats along a 7.25 m line were sampled at the channel site.

Community Productivity

Net apparent photosynthesis of the most abundant macrophytes found at the study sites was determined in a shallow current channel at ambient water temperatures (27 C) on 24 April 1980. Four replicate incubations per taxon were conducted between 0900 and 1430 hrs under a photon flux of 900 to 1900 micro Einsteins/m²/sec of photosynthetically active radiation (45,000 to 95,000 lux). This was the natural light in situ and within the range of light saturation values documented for other shallow macroalgal species (King and Schramm 1976; Arnold and Murray 1980; LaPointe et al. 1983). Net productivity was measured to 0.1 parts per million of dissolved oxygen by means of YSI Model 57 oxygen analyzer and calculated as milligrams carbon fixed per unit of thallus area per hour assuming a photosynthetic quotient of 1.00. To enable comparisons with other tropical marine ecosystems, daily daylight rates were approximated by multiplying the mean hourly rates by the number of daylight hours above the saturation intensity. All specimens used were from shallow locations in full sunlight. The methods concerning the selection of material, handling, incubation and oxygen analysis were within the limits recommended by Littler (1979) and Littler and Arnold (1980).

Analyses of Data

Data obtained by photogrammetric sampling enable quantification of the distributions and abundances of standing stocks in relation to transect distance and depth. All quadrat data were summed and averaged to yield mean cover values and used to interpret differences in macrophyte populations and communities between sites. The two-dimensional (i.e. planar area intercepting the light) species cover per square meter of substratum in conjunction with individual productivities per square meter of planar thallus area were multiplied to estimate the contribution of each abundant macrophyte to overall community production.

Diversity measurements have been widely employed by those responsible for assessing the effects of disturbances on biotic communities. Species diversity is often measured by indices (see Poole 1974 or Pielou 1975 for references and definitions) that include components of both species richness and equitability (the evenness with which the individuals are apportioned among species. The problem with any single index is that both the richness and equitability components of diversity are confounded. Many diversity indices also

contain the underlying assumption that the ecological importance of a given species is proportional to its abundance. We avoided these problems by using the commonly-applied Shannon and Weaver H' index (incorporating both richness and evenness) along with separate indices for richness (counts of taxa, Simpson's Index, Margalef's D') and evenness [equitability (E'), Pielou's J']. These were calculated for the cover data using natural logarithms of macrophyte cover and used as supplementary information to provide between-site comparisons of community structure.

To characterize natural species assemblages within each site grouping in an unbiased manner, the cover data for all quadrats were subjected to hierarchical cluster analyses (flexible sorting; Smith 1976) using the Bray and Curtis (1957) percentage distance statistic. This produced dendrograms of transect assemblages that were then interpreted according to their dominant biota and environmental affinities and used to map the prevalent zonal patterns for the two sites.

RESULTS

The channel site exceeded the bay site in all measured parameters (cover, productivity and diversity; Table 1) except species richness. Parameters for which the channel site was higher were as follows: total cover (1.5 times), total benthic community primary productivity (1.3X), Pielou's evenness index (J' , 1.2X) and equitability (E' , 1.5X). Conversely, Margalef's richness index (D') was 1.8 times higher at the bay site, while Simpson's index was 1.2 times greater. Shannon-Weaver diversity values (H') for the two sites were nearly equal, since the higher richness at the bay site balanced the greater evenness at the channel area.

Five species comprised 96% of the cover at the bay site (Table 2), led by Halimeda opuntia f. triloba (Decaisne) Barton (37%) and Thalassia testudinum Banks and König (26%); whereas, H. opuntia f. triloba (40%), Amphiroa fragilissima (Linnaeus) Lamouroux (22%) and T. testudinum (16%) provided the majority of the total community productivity. At the channel site (Table 3), six taxa contributed 96% of the cover, dominated by a filamentous, gelatinous diatom species (29%) and Caulerpa verticillata J. Agardh (28%). Major primary producers at the channel site were the three cover dominants, the gelatinous diatom (24% of the total community carbon fixed), C. verticillata (22%) and H. opuntia f. triloba (20%).

The cluster plots (Figs. 2 and 3) reveal distinctly different zonal patterns between the two sites. The bay site is characterized by (1) the Caulerpa/Halimeda assemblage forming a band nearest the mangrove roots which intergrades into (2) a zone dominated by the Halimeda/Dictyota assemblage. This last cluster group, in conjunction with (3) an assemblage characterized by the corallines Amphiroa and Neogoniolithon, forms a third zone, while the fourth most-seaward zone is delineated by the dominance of (4) a Thalassia/Halimeda assemblage. The channel site also contained four zonal assemblages as follows, proceeding from the edge of the mangrove

island toward the main channel: (1) a gelatinous diatom-dominated group overlying C. verticillata in very silty substrata nearest the mangrove roots, with Halimeda also present more channelward, (2) a Spyridia/Halimeda assemblage, followed by (3) a zone dominated by the Halimeda spp. cluster and, lastly, (4) a Thalassia assemblage that continues on across the Twin Cays main channel (Fig. 1).

In terms of production rates per square meter of thallus planar area (Fig. 4), the corallines Neogoniolithon strictum (Foslie) Setchell and Mason (0.38 g carbon/m²/h) Amphiroa fragilissima (0.29) and Amphiroa rigida Lamouroux var. antillana Børgesen (0.29) were highest, followed by the calcareous green alga Penicillus pyriformis A. & E.S. Gepp (0.19). In terms of production per unit of substratum, the channel site was nearly 1.3 times more productive on the average than the bay site, led by the gelatinous diatom (4.1 g carbon/m² of substratum/day). In contrast, the siphonaceous green alga, Halimeda opuntia f. triloba was by far the greatest contributor to community productivity (5.4 g C/m²/d) at the bay site.

DISCUSSION

Although the seagrass Thalassia testudinum was a conspicuous component of the florae at both sites, algae collectively were the predominant organisms (cf. Tables 2 and 3), providing 73.8% of the plant cover and 83.6% of the productivity at the bay site and 89.9% and 92.4% of the total plant cover and productivity at the channel site, respectively. The filamentous-group dominated production at the channel site; whereas, the soft-bottom siphonaceous algal forms provided the majority of production at the bay site. The overall community contribution of the seagrass was more than double in terms of both cover (26.2% vs. 10.1%) and productivity (16.4% vs 7.6%) at the bay site.

McRoy and Lloyd (1981) have contrasted marine macrophytes into two fundamentally different groups: (1) the macroalgae and (2) the seagrasses. The former group, according to these authors, is characterized as analogous to filter feeding animals (in their extraction of nutrients) while secured to two-dimensional hard substrata by means of a holdfast. The latter extract nutrients from both the water column and soft sedimentary, three-dimensional substrata by means of vascular root-rhizome systems that also serve to anchor them. This dichotomy ignores the many siphonaceous algal forms that we have shown (Tables 2 and 3) to be prevalent in association with Twin Cays mangrove islands. These algae, mainly of the order Caulerpales, also have root-like and rhizomatous systems for attachment in soft substrata and, because cross walls are minimal, can utilize cytoplasmic streaming to translocate nutrients taken up from both the sedimentary and aquatic milieu.

In terms of the predominant marine plant functional groups (Table 4), the Jointed-Calcareous-Group dominated the bay site with 48.6% of the total cover, followed by the Thick Leathery-Group (26.0%), Sheet-Group (12.6%), Filamentous-Group (11.7%), Crustose-Group (1.2%) and Coarsely-Branched-Group (0.1%). The Jointed-Calcareous-Group also

contributed a disproportionately large amount to the total marine macrophytic productivity (63.1%), the order of importance to production of the remaining groups was the same as for cover (Thick-Leathery, 16.1%; Sheet, 9.7%; Filamentous, 7.5%; Crustose, 3.4%; Coarsely-Branched, 0.1%). Members of the Sheet-Group and the Crustose-Group were largely absent from the channel site. For the channel site, the Filamentous-Group contributed the majority of total community cover (64.9%) as well as productivity (58.6%), whereas the Jointed-Calcareous-Group ranked second (20.8% of total cover and 29.8% of total productivity) and the Thick-Leathery-Group was third (10.2% of cover and 7.6% of productivity, respectively). Coarsely-Branched- and Crustose-Groups were minor components at both sites.

The two macrophyte communities are essentially quite similar (Tables 2 & 3), with the majority of differences (e.g. cover, productivity, evenness and richness; Table 1) due to the epiphytic overstory contributed by the Filamentous-Group at the sheltered channel site. This extensive mat-like canopy of a very delicate, filamentous/gelatinous diatom and weakly anchored Caulerpa verticillata may be very susceptible to wave damage at the more northerly, exposed bay site. We observed mats of the diatom being torn loose by the action of a boat wake on one occasion. The poor biomechanical resistance of filamentous algae has been documented for both temperate habitats (Littler and Littler 1980) and biotic reefs (Littler, Littler and Taylor 1983).

Mangrove island mud banks, such as those studied here, tend to be depauperate in regard to the photosynthetic corals, the Sheet-Group of macrophytes, non-calcified frondose forms (i.e. Coarsely-Branched- and Thick-Leathery-Group) and the Crustose-Group. In contrast, on hard-surfaced carbonate reefs (Littler and Littler 1984), corals, non-articulated coralline algae (Crustose-Group) and/or various small microscopic forms (Filamentous-Group) usually comprise the major cover. Larger non-calcareous frondose macrophytes (Sheet-, Coarsely-branched-, Thick-leathery-Groups) occur abundantly on reef flats (Doty 1971; Wanders 1976; Connor and Adey 1977), unstructured sand plains (Earle 1972; Dahl 1973; Hay 1981a) or deep-water sites (Littler et al. 1985) where herbivory is very low.

The inconspicuousness of non-calcified algae on many shallow reef-front systems is thought (Randall 1961; Wanders 1977; Borowitzka 1981) to result primarily from intensive grazing by the numerous herbivores and omnivores inhabiting these spatially heterogeneous systems. Where spatial heterogeneity (i.e. protective cover for fishes and sea urchins) is minimal on tropical reefs, herbivore activity is relatively low (Connor and Adey 1977; Brock 1979; Hay et al. 1983) and reasonably large standing stocks of macrophytes often develop (Doty 1971; Tsuda 1971; Connor and Adey 1977; Wanders 1976). On Twin Cays, the shallow bordering mud flats are extremely low in spatial heterogeneity, with the macrophytes themselves comprising most of the three-dimensional structure. Barracuda (Sphyraenidae), mangrove snapper (Lutjanidae), jacks (Carangidae) and other fishes are abundant predators near the channels and hanging roots of mangrove islands (personal observations), and this undoubtedly contributes to the reduced levels of herbivorous fishes.

Sea urchins can be locally abundant within the mangrove root habitat and often produce a grazing halo (cf. Ogden et al. 1973) that tends to be dominated by grazer-resistant (Paul and Fenical 1983) species of Halimeda (Figs. 4 & 5) adjacent to and between the Rhizophora mangle. Thalassia testudinum with other interspersed seagrasses and Caulerpaes become abundant beyond the feeding ranges of urchins unless an eroded bank prevents such a transition. Sea urchins were numerous among the mangrove roots at the bay site and moved onto the algal/seagrass flats at night. Total sea urchin density in the vicinity of the bay site was $4.4 \cdot m^{-2}$, comprised mostly of Echinometra viridis Agassiz, E. lacunata (L.) and Lytechinus variegatus (Lamarck), with Diadema antillarum Philippi, Eucidaris tribuloides (Lamarck) and Tripneustes ventricosa (Lamarck) also present. During approximately 20 person-hours of searching, no urchins were encountered in the vicinity of the channel site. Other research (Taylor, Littler and Littler, submitted) indicates that such differences in herbivory may, in conjunction with the physical action of waves mentioned above, account for the reduction of delicate filamentous forms and epiphytes and the predominance of herbivore-resistant macrophytes at the bay site.

Such resistant plant populations often contribute (Rogers and Salesky 1981) a major portion of the total primary productivity of some reefs. However, most evidence (e.g. Wanders and Wanders-Faber 1974, Bunt 1975, Marsh 1976, Dahl 1976 Larkum 1981, Rogers and Salesky 1981) indicates that it is the fast-growing and opportunistic filamentous algae of sparse mats that result in the very high primary production rates per unit area of most biotic reefs. Conversely, tightly-compacted mats of algae (turfs), such as those of the channel site, usually show reduced productivity levels (Littler and Arnold 1980, Hay 1981b, Taylor and Hay 1984) due to overlapping diffusion gradients and self shading.

The total community primary productivity at the channel site was 28% higher than at the bay site (17.2 vs. $13.4 \text{ g C fixed} \cdot m^{-2} \text{ of substratum} \cdot d^{-1}$). This difference was largely due to the contributions of the filamentous/gelatinous diatom ($4.1 \text{ g C fixed} \cdot m^{-2} \cdot d^{-1}$) and Spyridia filamentosa (2.2), epiphytes that were not abundant at the bay site.

The macrophytic daylight community productivities at both sites were quite high relative to reef systems and compare favorably with the upper rates reported from dense seagrass meadows (Table 5). Reported daily primary productivities of seagrass communities span the upper range from 5.8 to $18.7 \text{ g carbon} \cdot m^{-2} \cdot d$. Rates reported for reef systems range upwards to $7.2 \text{ g C} \cdot m^{-2} \cdot d$. We conclude that mud reef-flats adjacent to the mangrove islands of the Belize barrier reef system produce at rates comparable to dense seagrass beds and are considerably more productive than typical carbonate reef-flat habitats. This high photosynthetic capacity may be related to reductions in herbivory, enabling larger standing stocks to develop, and the recycling of nutrients from decompositional processes, which would be expected to augment the primary productivity of these otherwise nutrient-impovertished waters.

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REFERENCES

- Arnold, K. E. and S. N. Murray. 1980. Relationships between irradiance and photosynthesis for marine benthic green algae (Chlorophyta) of differing morphologies. *J. Exp. Mar. Biol. Ecol.* 43: 183-192.
- Bakus, G. J. 1967. The feeding habits of fishes and primary production at Eniwetok, Marshall Islands. *Micronesica* 3: 135-149.
- Borowitzka, M. A. 1981. Algae and grazing in coral reef ecosystems. *Endeavour*, 5: 99-106.
- Brawley, S. H. and W. H. Adey. 1977. Territorial behavior of threespot damselfish (Eupomacentrus planifrons) increases reef algal biomass and productivity. *Envir. Biol. Fish.* 2: 45-51.
- Bray, J. R. and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27: 325-349.
- Brock, R. E. 1979. An experimental study on the effects of grazing by parrotfishes and role of refuges in benthic community structure. *Mar. Biol.* 51: 381-388.
- Buesa, R. J. 1972. Production primaria de las praderas de Thalassia testudinum de la plataforma noroccidental de Cuba. INP, Cuba Cent. Inv. Pesqueras. *Reva. Bal. Trab. CIP*, 3: 101-143.
- Bunt, J. S. 1975. Primary productivity of marine ecosystems. In: H. Lieth and R. H. Whittaker (Eds.), *Primary Productivity of the Biosphere*. Ecological Studies, Springer-Verlag, Berlin 14: 169-183.
- Connor, J. L. and W. H. Adey. 1977. The benthic algal composition, standing crop, and productivity of a Caribbean algal ridge. *Atoll. Res. Bull.* 211: 1-15.
- Dahl, A. L. 1972. Ecology and community structure of some tropical reef algae in Samoa. Pages 36-39, in K. Nisizawa (Ed.), *Proceedings of the Seventh International Seaweed Symposium*. University of Tokyo Press, Tokyo, Japan.

- Dahl, A. L. 1973. Surface area in ecological analysis: quantification of benthic coral-reef algae. *Mar. Biol.*, 23: 239-249.
- Dahl, A. L. 1976. Generation of photosynthetic surface area by coral reef algae. *Micronesica* 12: 43-47.
- Doty, M. S. 1971. Physical factors in the production of tropical benthic marine algae. Pages 99-121 in J. D. Costlow, Jr., (Ed.) *Fertility of the Sea*. Gordon and Breach, New York.
- Earle, S. A. 1972. The influence of herbivores on the marine plants of Great Lameshur Bay, with an annotated list of plants. Pages 17-44 in B. B. Collette and S. A. Earle (Eds.), *Results of the Tektite Program: Ecology of Coral Reef Fishes*, Science Bulletin 14, Los Angeles County Natural History Museum, Los Angeles, California.
- Gaines, S. D. and J. Lubchenco. 1982. A unified approach to marine plant-herbivore interactions. II. Biogeography. *Ann. Rev. Ecol. Syst.* 13: 111-138.
- Gessner, F. and L. Hammer. 1960. Die primarproduktion in Mediterranean Caulerpa-Cymodocea Wiesen. *Bot. Mar.* 2: 157-163.
- Hatcher, B. G. 1982. The interaction between grazing organisms and the epilithic algal community of a coral reef: a quantitative assessment. Pages 515-524 in E. D. Gomez et al. (Eds.), *Proceedings, Fourth International Coral Reef Symposium*, Marine Science Center, Quezon City, Philippines
- Hatcher, B. G. and A. W. D. Larkum. 1983. An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. *J. Exp. Mar. Biol. Ecol.* 69: 61-84.
- Hay, M. E. 1981a. Herbivory, algal distribution, and the maintenance of between-habitat diversity on a tropical fringing reef. *Am. Nat.* 118: 520-540.
- Hay, M. E. 1981b. The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. *Ecology* 62: 739-750.
- Hay, M. E., T. Colburn and D. Downing. 1983. Spatial and temporal patterns in herbivory on a Caribbean fringing reef: the effects on plant distribution. *Oecologia* (Berlin) 58: 299-308.
- Johnston, C. S. 1969. The ecological distribution and primary production of macrophytic marine algae in the eastern canaries. *Int. Revue ges. Hydrobiol.* 54: 473-490.
- King, R. J. and W. Schramm. 1976. Photosynthetic rates of benthic marine algae in relation to light intensity and seasonal variations. *Mar. Biol.* 37: 215-222.

- LaPointe, B. E., K. R. Tenore and C. J. Dawes. 1983. Interactions between light intensity and temperature on the physiological ecology of Gracilaria tikvahiae (Gigartinales, Rhodophyta). I. Growth, photosynthesis, and respiration. Mar. Biol.
- Larkum, A. W. D. 1981. Marine primary productivity. Pages 370-385 in M. N. Clayton and R. J. King (Eds.), Marine Botany, an Australasian Perspective. Longman Cheshire, Melbourne.
- Littler, M. M. 1973a: The population and community structure of Hawaiian fringing-reef crustose Corallinaceae (Rhodophyta, Cryptonemiales). J. Exp. Mar. Biol. Ecol. 11: 103-120.
- Littler, M. M. 1973b. The productivity of Hawaiian fringing-reef crustose Corallinaceae and an experimental evaluation of production methodology. Limnol. Oceanogr. 18: 946-952.
- Littler, M. M. 1979. The effects of bottle volume, thallus weight, oxygen saturation levels, and water movement on apparent photosynthetic rates in marine algae. Aquat. Bot. 7: 21-34.
- Littler, M. M. and K. E. Arnold. 1980. Sources of variability in macroalgal primary productivity: sampling and interpretative problems. Aquat. Bot. 8: 141-156.
- Littler, M. M. and K. E. Arnold. 1982. Primary productivity of marine macroalgal functional-form groups from southwestern North America. J. Phycol. 18: 307-311.
- Littler, M. M. and D. S. Littler. 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. Am. Nat. 116: 25-44.
- Littler, M. M. and D. L. Littler. 1984. Biogenesis of tropical reefs: the contribution of algae. In: F. E. Round and D. J. Chapman (Eds.), Progress in Phycological Research, 3: (in press).
- Littler, M. M., D. S. Littler, S. M. Blair and J. N. Norris. 1985. Deepest known plant life discovered on an uncharted seamount. Science 227: 57-59.
- Littler, M. M., D. S. Littler and P. R. Taylor. 1983. Evolutionary strategies in a tropical barrier reef system: functional-form groups of marine macroalgae. J. Phycol. 19: 229-237.
- Littler, M.M. and S.N. Murray. 1975. Impact of sewage on the distribution, abundance and community structure of rocky intertidal macro-organisms. Mar. Biol. 30: 277-291.
- Marsh, J. A., Jr. 1976. Energetic role of algae in reef ecosystems. Micronesica 12: 13-21.

- McRoy, C. P. and D. S. Lloyd. 1981. Comparative function and stability of macrophyte-based ecosystems. Pages 473-489 in A. R. Longhurst (Ed.), Analysis of marine ecosystems. Academic Press, New York.
- Murray, S. N. and M. M. Littler. 1984. Analysis of seaweed communities in a disturbed rocky intertidal environment near Whites Point, Los Angeles, Calif. U.S.A. In: Proceedings, Eleventh International Seaweed Symposium, Qingdao, China. Hydrobiologia, (in press).
- Odum, H. T. 1963. Productivity measurements in Texas Turtle grass and the effects of dredging an intracoastal channel. Publ. Inst. Mar. Sci. Texas 9: 45-58.
- Odum, H. T. and C. M. Hoskin. 1958. Comparative studies of the metabolism of marine waters. Publ. Inst. Mar. Sci. Univ. Texas 5: 16-46.
- Odum, H. T. and E. P. Odum. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecol. Monogr. 25: 291-320.
- Ogden, J. C., R. A. Brown and N. Selesky. 1973. Grazing by the echinoid Diadema antillarum Philippi: formation of halos around West Indian patch reefs. Science 182: 715-717.
- Paul, V. J. and W. Fenical. 1983. Isolation of halimedaerial: chemical defense adaptation in the calcareous reef-building alga Halimeda. Science 221: 747-749.
- Pielou, E. 1975. Ecological diversity. John Wiley and Sons, New York, New York.
- Poole, R. W. 1974. An introduction to quantitative ecology. McGraw-Hill, New York, New York.
- Qasim, S. Z. and P. M. A. Bhattathiri. 1971. Primary production of a seagrass bed on Kavaratti Atoll (Laccadives). Hydrobiologia 38: 29-38.
- Randall, J. E. 1961. Overgrazing of algae by herbivorous marine fishes. Ecology 42: 812.
- Rützler, R. and I. G. MacIntyre (Eds.) 1982. The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize, I. Structure and Communities. Smithsonian. Contrib. Mar. Sci., No. 12. Smithsonian Institution Press, Washington, D.C.
- Rogers, G. S. and N. H. Salesky. 1981. Productivity of Acropora palmata (Lamarck), macroscopic algae, and algal turf from Tague Bay Reef, St. Croix, U.S. Virgin Islands. J. Exp. Mar. Biol. Ecol. 49: 179-187.

- Smith, R. W. 1976. Numerical Analysis of Ecological Survey Data. Ph.D. dissertation, University of Southern California, Los Angeles.
- Smith, S. V. 1973. Carbon dioxide dynamics: a record of organic carbon production, respiration, and calcification in the Eniwetok reef flat community. *Limnol. Oceanogr.* 18: 106-120.
- Sournia, A. 1976. Oxygen metabolism of a fringing reef in French Polynesia. *Helgoländer wiss. Meeresunters.* 28: 401-410.
- Steneck, R. S. and L. Watling. 1982. Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. *Mar. Biol.* 68: 299-319.
- Taylor, P. R. and M. E. Hay (in press). The functional morphology of intertidal seaweeds: the adaptive significance of aggregate vs. solitary forms. *Mar. Ecol. Prog. Ser.*
- Taylor, P. R., M. M. Littler and D. S. Littler (in review). Coexistence and non-coexistence escapes of herbivory as structuring forces in mangrove island macroalgal communities. *Ecology*.
- Tsuda, R. T. 1971. Morphological, zonal, and seasonal studies of two species of Sargassum on the reefs of Guam. Pages 40-44 in K. Nisizawa (Ed.), *Proceedings, Seventh International Seaweed Symposium*. Wiley & Sons, New York.
- Van Den Hoek, C., A. M. Cortel-Breeman and J. B. W. Wanders. 1975. Algal zonation in the fringing coral reef of Curacao, Netherlands Antilles, in relation to zonation of corals and gorgonians. *Aquat. Bot.* 1: 269-308.
- Wanders, J. B. W. 1976. The role of benthic algae in the shallow reef of Curacao (Netherlands Antilles). I: primary production in the coral reef. *Aquat. Bot.* 2: 235-270.
- Wanders, J. B. W. 1977. The role of benthic algae in the shallow reef of Curacao (Netherlands Antilles) III: the significance of grazing. *Aquat. Bot.*, 3: 357-390.
- Wanders, J. B. W. and A. Wanders-Faber. 1974. Primary productivity of the S.W. coast shallow reef and the N.E. coast brown algae of Curacao. *Br. Phycol. J.* 9: 223-224.

Table 1. Indices of richness, evenness and diversity, based on macrophytic species numbers and cover, for the bay and channel sites.

Indices	Bay	Channel
H' index	2.32	2.39
J' evenness	0.85	1.00
E' equitability	0.64	0.99
D' richness	2.52	1.44
Number of species	14	11
Simpsons index	0.11	0.09
Total cover	97.8	151.8
Total productivity (g carbon/m ² /d)	13.4	17.2

Table 2. The major contributors of community cover and primary productivity (g carbon/m²/d) at the bay site.

Taxa	Cover (%)	Productivity (m ² of substratum)
<u>Halimeda opuntia</u> f. <u>triloba</u> (Decaisne) Barton	36.1	5.4
<u>Thalassia testudinum</u> Banks & K��nig	25.6	2.2
<u>Dictyota dichotoma</u> (Hudson) Lamouroux	12.4	1.3
<u>Caulerpa verticillata</u> J. Agardh	11.2	1.0
<u>Amphiroa fragilissima</u> (Linnaeus) Lamouroux	10.0	2.9
<u>Neogoniolithon strictum</u> (Foslie) Setchell & Mason	1.2	0.5
<u>Halimeda monile</u> (Ellis & Solander) Lamouroux	0.4	0.07
<u>Dasya rigidula</u> (K��ltz.) Ardiss.	0.4	--
<u>Amphiroa rigida</u> Lamouroux var. <u>antillana</u> B��rgesen	0.3	0.09
<u>Valonia ventricosa</u> J. Agardh	0.07	--
<u>Wrangelia</u> sp.	0.04	--
<u>Hypnea</u> sp.	0.02	--
<u>Penicillus capitatus</u> Lamarck	0.02	0.01
<u>Dictyosphaeria cavernosa</u> (Forssk.) B��rgesen	0.02	0.01
Totals	97.8	13.4

Table 3. The major contributors of community cover and primary productivity (g carbon/m²/d) at the channel site.

Taxa	Cover (%)	Productivity (m ² of substratum)
Gelatinous diatom	43.6	4.1
<u>Caulerpa verticillata</u> J. Agardh	41.9	3.8
<u>Halimeda opuntia</u> f. <u>triloba</u> (Decaisne) Barton	22.6	3.4
<u>Thalassia testudinum</u> Banks & König	15.4	1.3
<u>Spyridia filamentosa</u> (Wulfen) Harvey	13.2	2.2
<u>Halimeda monile</u> (Ellis & Solander) Lamouroux	9.0	1.5
<u>Penicillus capitatus</u> Lamarck	2.8	0.3
<u>Dictyosphaeria cavernosa</u> (Forssk.) Børgesen	2.7	0.3
<u>Caulerpa mexicana</u> (Sound.) J. Agardh	0.5	0.04
<u>Amphiroa fragilissima</u> (Linnaeus) Lamouroux	0.08	0.2
<u>Penicillus pyriformis</u> A. & E.S. Gepp	0.08	0.02
Totals	151.8	17.2

Table 4. Functional-group categories and major component taxa.

Functional Groups	Characteristics	Taxa
Filamentous-Group	Thin, uniseriate, multiseriate or lightly corticated	Gelatinous diatom, <u>Caulerpa verticillata</u> , <u>Dasya rigidula</u> , <u>Spyridia filamentosa</u> , <u>Wrangelia</u> sp.
Sheet-Group	Uncorticated, foliose	<u>Dictyota dichotoma</u>
Coarsely-Branched-Group	Corticated	<u>Caulerpa mexicana</u> , <u>Dictyosphaeria cavernosa</u> , <u>Hypnea</u> sp., <u>Penicillus capitatus</u> , <u>Penicillus pyriformis</u> , <u>Valonia ventricosa</u> ,
Thick-Leathery-Group	Differentiated, heavily corticated, thick walled	<u>Thalassia testudinum</u>
Jointed-Calcareous-Group	Calcified genicula, uncalcified intergenicula	<u>Amphiroa fragilissima</u> , <u>Halimeda monile</u> , <u>Halimeda opuntia</u> f. <u>triloba</u>
Crustose-Group	calcified or uncalcified parallel cell rows, encrusting	<u>Neogoniolithon strictum</u>

Table 5. Comparative upper production rates of macrophyte communities in tropical marine shallow water ecosystems.

Community type	Productivity g carbon/m ² d	Location	Study
Mangrove banks			
channel	17.2	Belize	This study
bay	13.4	Belize	This study
Seagrass Meadows			
<u>Cymodocea nodosa</u> K.D.E. König dominant	18.7	Mediterranean	Gessner & Hammer, 1960
<u>Syringodium isoetifolius</u> Archers and Graeb dominant	5.8	Laccadives	Qasim & Bhattathiri, 1971
<u>Thalassia testudinum</u> dominant	12.5	Cuba	Buesa, 1972
<u>Thalassia testudinum</u> dominant	16.0	Florida	Odum, 1963
<u>Thalassia testudinum</u> dominant	9.0	Texas	Odum & Hoskin, 1958
Carbonate Reefs			
Shallow fore and back reefs, algal turf dominated	5-7	St. Croix Virgin Is.	Brawley & Adey, 1977
Fringing reef, <u>Neogoniolithon frutescens</u> dominated	3.8	French Polynesia	Sournia, 1976
Intertidal, blue green algae dominated	0.65-2.15	Enewetak	Bakus, 1976
Macroalgal dominated	1.5 -3.0	Canary Is.	Johnston, 1965
Photosynthetic corals and algal turfs	1.6-7.2	Enewetak	Smith, 1973

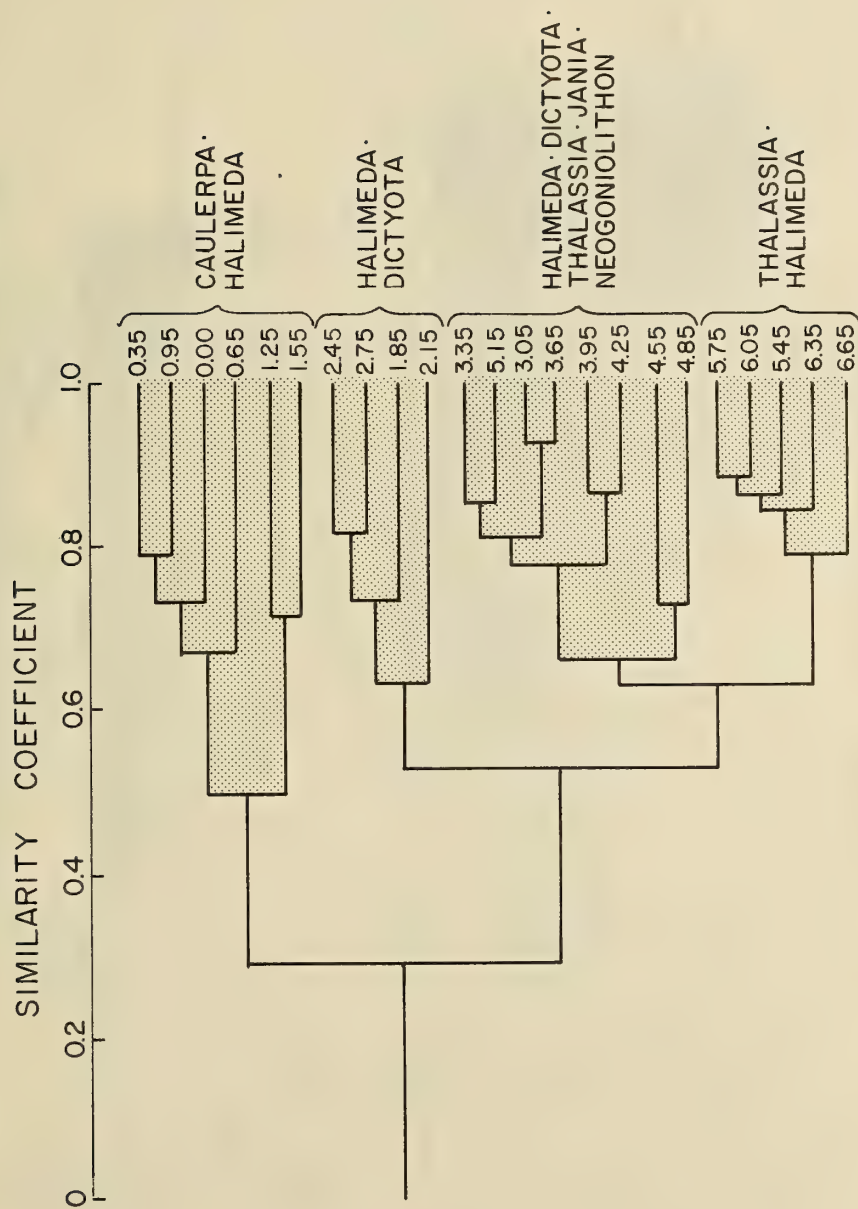


Figure 2. Cluster analysis based on percentage cover data for the bay site quadrats (labelled by distance along transect in meters) expressed as a dendrogram. Dominant cover organisms in each cluster group are given on the right.

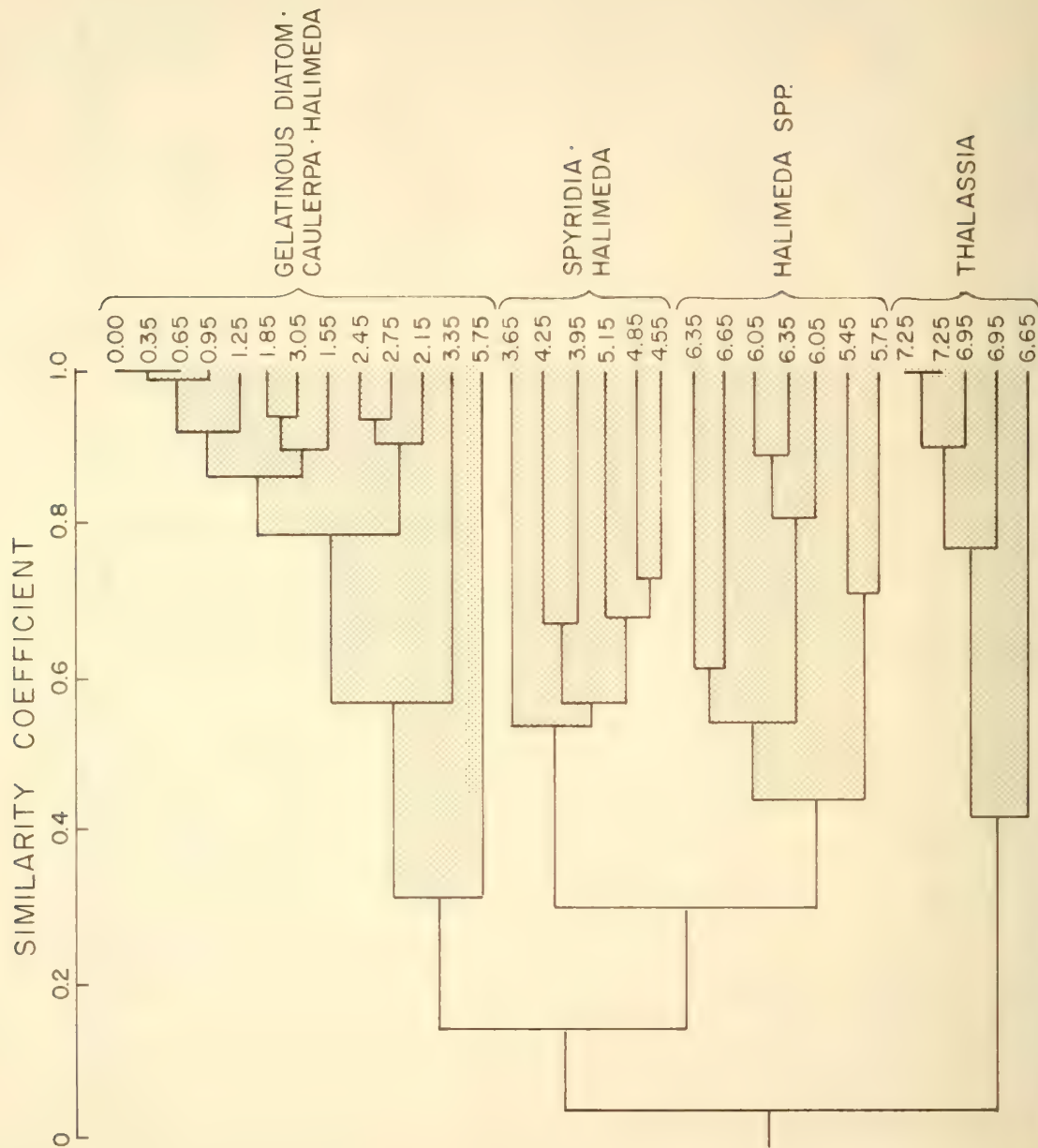


Figure 3. Cluster analysis based on percentage cover data for the channel site quadrats (labelled by distance along transect in meters) expressed as a dendrogram. Dominant cover organisms in each cluster group are given on the right.

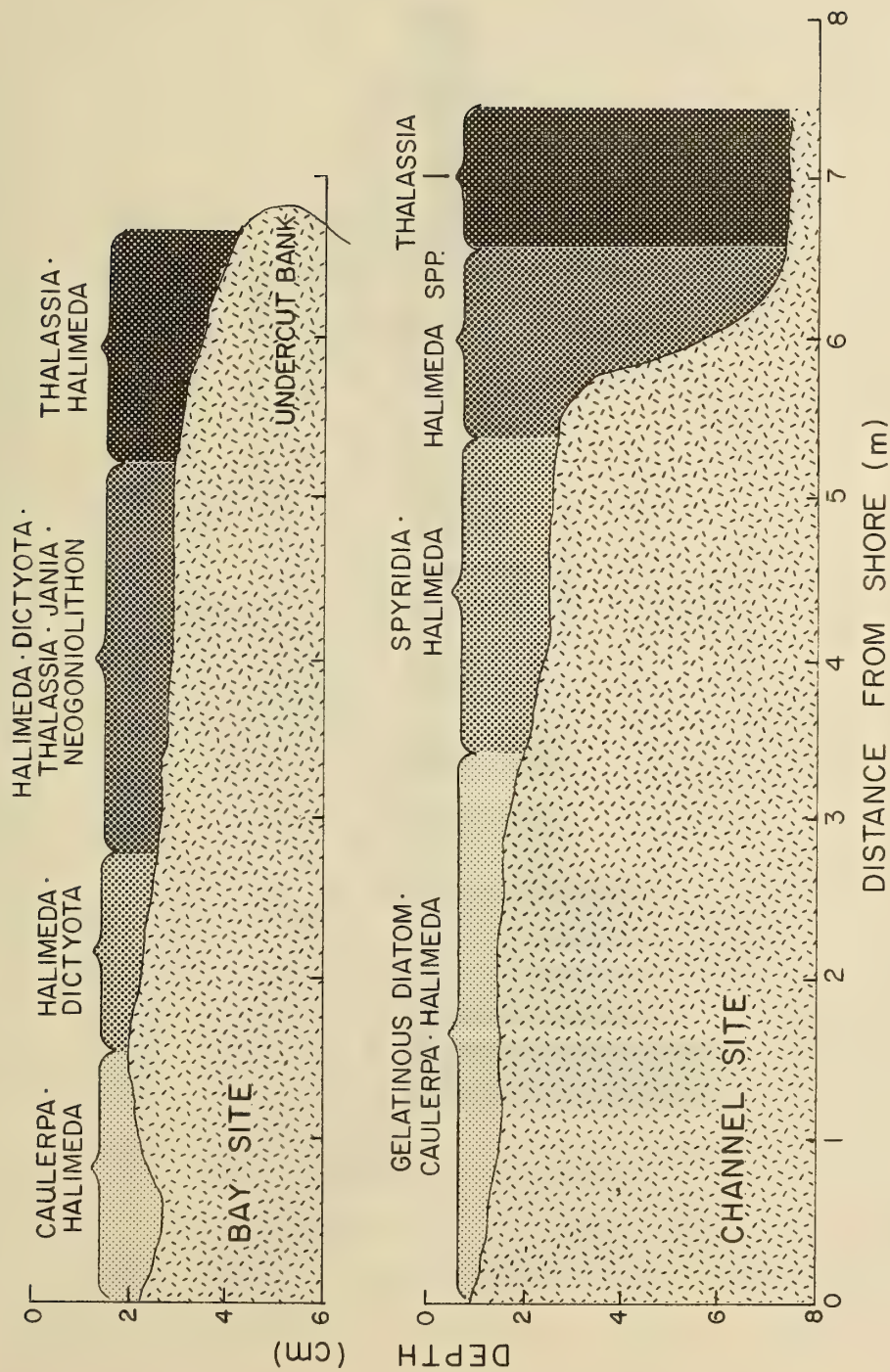


Figure 4. Diagrammatic locations of dominant cluster groups (determined from Figs. 2 & 3) in relation to depth profile and distance along the shoreline at the bay site (upper plot) and channel site (lower plot).

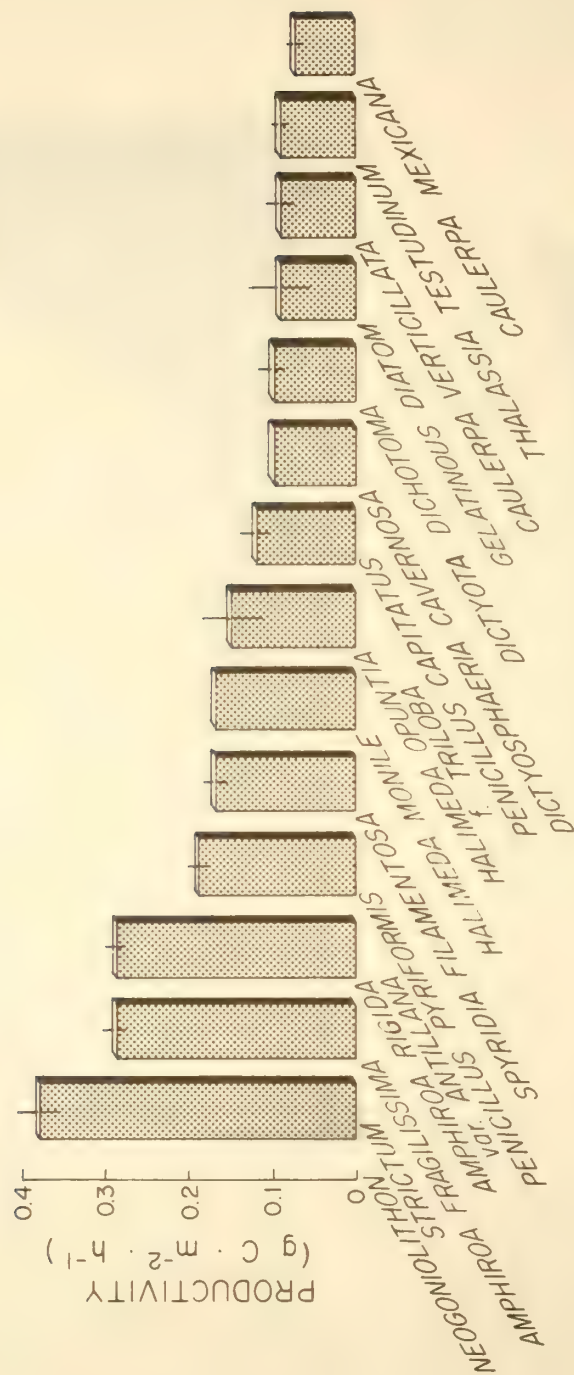


Figure 5. Net apparent primary productivities (m^{-2} substratum) of dominant macrophytes from Twin Cays on 24 April 1980. $\pm 95\%$ confidence limits given by vertical lines.

ATOLL RESEARCH BULLETIN

No. 290

SOME OBSERVATIONS ON NESILLAS ALDABRANUS, THE
ENDANGERED BRUSH WARBLER OF ALDABRA ATOLL,
WITH HYPOTHESES ON ITS DISTRIBUTION

By

C. HAMBLER, K. HAMBLER AND J. M. NEWING

ISSUED BY

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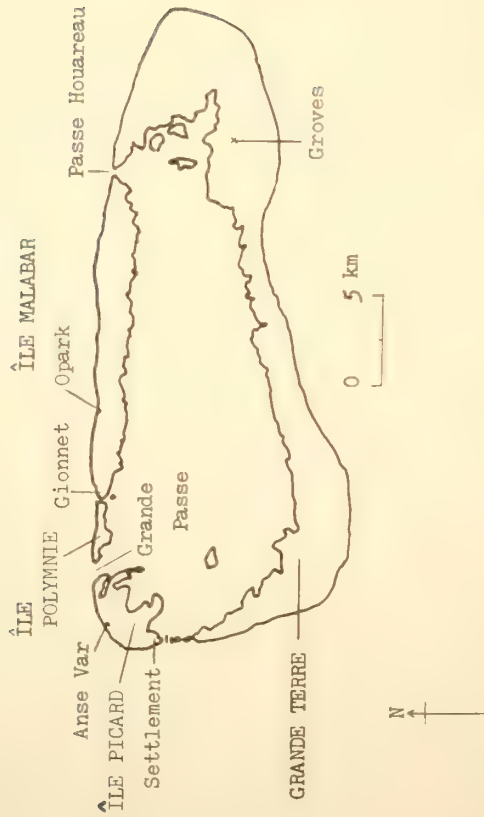
WASHINGTON, D. C., U.S.A.

MAY 1985

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ALDABRA ATOLL



NOTES:

G.S.A. denotes Gionnet Study Area

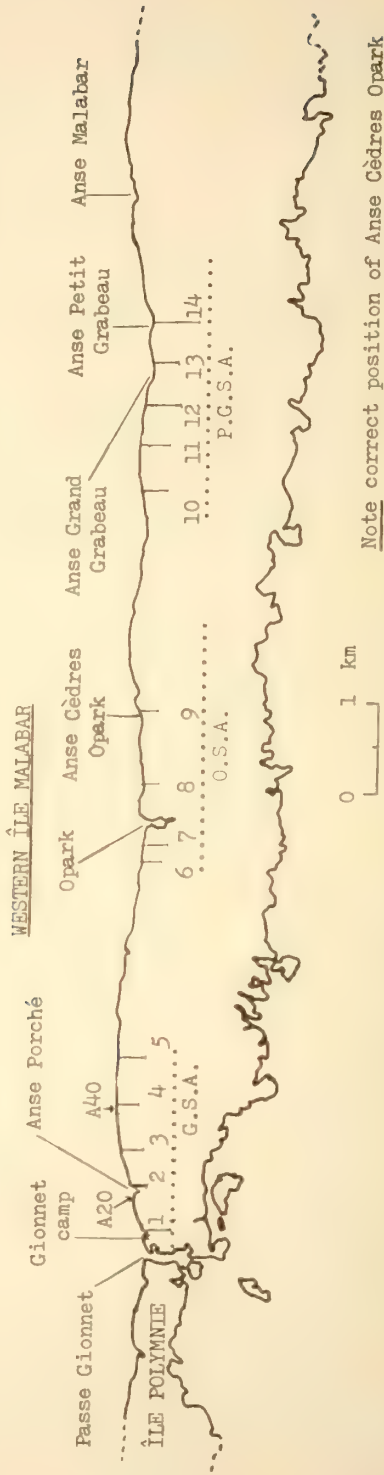
O.S.A. denotes Opark Study Area

P.G.S.A. denotes Anse Petit Grabeau Study Area

..... denotes east/west extent of Study Area

A20 shows position of numbered post on coastal 'A' path

[] shows approximate position of vegetation transect within penetrable mixed scrub



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C. HAMBLER*, K. HAMBLER AND J. M. NEWING

INTRODUCTION

Nesillas aldabranus Benson and Penny, the Aldabran Brush Warbler, is endemic to Aldabra atoll, Republic of Seychelles. It is considered the world's rarest, most restricted and most highly threatened bird (Collar and Stuart 1985).

This paper presents relatively recent observations of N. aldabranus, and considers the features of its habitat which may be involved in the very restricted distribution of this species on Aldabra. Testable hypotheses are presented which could form the basis of future work on this species, and which might help in efforts to conserve it.

The warbler was discovered in 1967 (Benson and Penny 1968), and as much of the atoll had already been sampled by mist-netting it was evident at that time that the species was not distributed throughout Aldabra. Extensive searches by R. P. Prŷs-Jones, between July 1974 and Feb. 1977, revealed five individuals; all were within a 50 m wide, 2 km long strip along the northern coast of western Ile Malabar near Gionnet (see Fig. 1). This strip will be called the Gionnet region, and the vegetation within it the classic habitat of N. aldabranus. No warblers have ever been seen away from their classic habitat, but it was hoped that the little-known southwestern region of Grande Terre might support a population; however, it is now known that the mixed scrub in the SW is dissimilar to that at Gionnet (Cowx 1980, D. McC. Newbery pers. comm. and personal observation) and limited searches with call playback revealed no warblers (C. Peet pers. comm.; personal observation 1983). It is thus considered unlikely that a population of N. aldabranus exists elsewhere than on Ile Malabar.

The population of the warbler was estimated to be at most 25 individuals in 1977, based on knowledge of behaviour and extrapolation into the extent of likely habitat (Prŷs-Jones 1979). The habitat considered suitable was that similar to the mixed scrub near the coast in the Gionnet region, and was thought to extend to ca. 1 km west of Anse Grand Grabeau.

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The classic habitat was considered to have four features which, taken in conjunction, made it distinct from other areas of the atoll (Prÿs-Jones 1979). These were :

- a) extremely dense, closed-canopy vegetation, with a considerable leaf litter/soil layer beneath;
- b) large, dense stands of almost pure Pandanus tectorius;
- c) a high abundance of Dracaena reflexa;
- d) a total absence of both tortoises (Geochelone gigantea Schweigger) and goats (Capra hircus L.)

In this paper we review these four features, considering recent observations of the warbler and using selected data from a study we made of the composition and architecture of the mixed scrub of Ile Malabar (which will be published separately).

We report here some observations on the warbler and related subjects made by the Animal Ecology Research Group, Oxford, Expedition to Aldabra (on Aldabra 2 Aug. to 26 Sept. 1981), the Southampton University Expedition to Aldabra (11 July to 15 Sept. 1982) and the Cambridge Aldabra Rail and Brush Warbler Expedition (19 July to 24 Sept. 1983).

I. RECENT OBSERVATIONS OF N. ALDABRANUS

1) Observations

Observations of the warbler up to 1977 are given in Benson and Penny (1968) and Prÿs-Jones (1979). Since R.P. Prÿs-Jones left Aldabra in 1977 there have been, to our knowledge, four definite records of N. aldabranus and a number of observations of birds thought to be of this species. These records are listed in Table 1. It has been pointed out by R.P. Prÿs-Jones (pers. comm.) that very occasionally vagrant warblers of other species may be found on Aldabra, and that although the long calls of N. aldabranus are distinct from the vocalisations of other indigenous birds (O.E. Prÿs-Jones, pers. comm.), confusion might conceivably arise with such vagrants; therefore, only good visual records can be treated as certain.

We describe some of the recent observations in detail below:

In 1981, whilst walking along uncut transects, C. Hamblen and T.C. Guilford heard a very distinctive call, subsequently identified by comparison with taped calls as almost certainly that of N. aldabranus. The site was in thick mixed scrub about 250 m east of Anse Petit Grabeau, and about 100 m inland close to vegetation dominated by Pemphis acidula. The call, lasting about two seconds, comprised a series of clicks in rapid succession; the frequency of clicking increased in the middle of the call, which was thus described non-phonetically as a "rattle, chirr, rattle". This may be the alarm call described by Penny as a harsh "chirrr" and by Diamond as a short, scolding chatter (in Benson and Penny, 1968).

On 1 Sept. 1983 at ca. 5 p.m. a chak sequence (Prÿs-Jones 1979) was heard three times by one of us (K.H.) in a thick Pemphis acidula bush, beside the northernmost pebble beach on the Malabar side of Passe Gionnet; several attempts were made to find this bird again in the following week,

including use of call playback and squeaking, but with no success.

On 2 Sept. in the early afternoon we heard two chak sequences between posts A28 and A29 on the coastal path at Gionnet. These calls, each lasting about 4 seconds, were probably the "machine-gun chatters" described by Prÿs-Jones (1979) as being given rarely, in excitement. The calling bird was seen, and it approached us--possibly attracted to squeaking. It did not respond to call playback and examined us from a distance of about a metre, before moving off and feeding in the scrub. The bird bore a single ring, on the right leg, so must have been one of the four birds ringed as adults in 1974; the colour ring on the left leg has been lost. Details of ringed birds are given by R.P. Prÿs-Jones (1979--for colour rings, and pers. comm.--for metal rings).

A warbler with a single ring, as above, was seen (by C.H.) around post A29 on 4 Sept., and between post A27 and A28 on 6 Sept. As other birds might have lost colour rings, we cannot be sure that the same individual was involved in each case.

In all the September 1983 sightings the bird was observed feeding actively; it appeared in good condition and was not in moult. In the sightings on 1 and 4 September the bird took many food items too small to identify, and was seen several times to hang beneath twigs and stems while pecking at the underside of leaves--such hanging behaviour was not observed by R.P. Prÿs-Jones (pers. comm.).

2) Discussion of recent observations

The recent observations are interesting mainly because of the extreme rarity of N. aldabranus; although they add little to what is already known of the species, any information is worth examining in case attempts can be made to save the bird, or as the last records of a species becoming extinct.

At least one of the birds ringed between 16 April 1974 and 17 Dec. 1974 survived in 1983, indicating that an age of at least 9 years can be reached. This is not exceptional for a small tropical bird (Prÿs-Jones and Diamond 1984). A mean life expectancy of 8.9 years is given for the Seychelles brush warbler (Acrocephalus sechellensis) by Diamond (1980), and individuals of that species have been observed engaged in breeding behaviour at 10 years old (V. Wood, per. comm.) with some surviving to at least 11 years (H. Owen, pers. comm.).

The bird(s) we saw on 2, 4, and 6 Sept. 1983 showed an initial interest in us, and then wandered off feeding; in the latter two sightings, squeaking and call playback were not used to attract the bird, and indeed in the first sighting of a bird on 2 Sept., we were not even seeking the bird when it first appeared near us. We had the distinct impression that the bird spontaneously approached people as they moved noisily through the vegetation on the path. It is therefore interesting that curiosity and tameness have been noted in the probable ancestor of N. aldabranus: the polytypic N. typica of Madagascar and the Comoro Islands (Rand 1936; Benson 1960). It is possible that when approaching in "curiosity" the bird is seeking disturbed invertebrates--perhaps also why

Nesillas is a common member of parties of mixed species on Grande Comoro (Benson 1960). As will be discussed later (Section II, 3) invertebrate abundance or activity may be crucial to the distribution of N. aldabranus.

All of the records of N. aldabranus fall within the Gionnet region, with the notable exception of that from near Anse Petit Grabeau in 1981, which is some 9 km east of the nearest previous record. As this record was of voice only, it is subject to the reservation mentioned above. The isolated observation of N. aldabranus here would present many interesting possibilities, but information on the species is so limited that interpretation is virtually pure speculation. It suggests that the warbler can at least survive in habitat not previously considered suitable. However, virtually nothing is known of dispersion in this species, other than that it may account for periods when individuals "vanished" from the study area at times between 1974 and 1977 (Prÿs-Jones 1979).

It is unlikely that a "sizeable" population (i.e. one as large as that of the Gionnet region in the 1974-1977 period) could have escaped detection in the Anse Petit Grabeau to Anse Malabar area, as this area has been visited many times on various research and management projects. We visited the area of the 1981 record in 1983, and used call playback and squeaking without result. If a population did exist there it would be less likely to be discovered if it were more than about 50 m inland, away from the coastal path, in more dense and less visited vegetation.

Our exploration of the Anse Petit Grabeau area in 1981 and 1983 revealed a mosaic of mixed scrub and patches of Pemphis, with the mixed scrub being closer in composition to "Malabar Mixed Scrub" than to "Gionnet and Polymnie Mixed Scrubs" (vegetation classification after Gibson and Phillipson 1983). Unless other observations of the warbler are made in the Anse Petit Grabeau region, or east of Opark, we believe there are insufficient grounds to include the vegetation in this region as suitable habitat for a population of N. aldabranus.

The nest we discovered west of Opark presents the possibility of the Gionnet population of N. aldabranus extending to Opark inlet, which would be consistent with the observations on vegetation discussed in Section II 1 below.

There are not enough data to compare the size of the population of warblers near Gionnet in the early 1980's with that in 1974-1977. The species is difficult to observe, and responds less readily to call playback in the dry season when our visits were made (R.P. Prÿs-Jones, pers. comm.). The recent infrequency of observations does not give an indication of a change in abundance, which could have occurred without detection. We discuss in the next section changes in the vegetation on Ile Malabar since the 1970's, which lead us to suggest that the maximum likely population is about half that previously estimated, without assuming a change in the real density of the species.

II. THE HABITAT OF N. ALDABRANUS

1) New observations on the vegetation of western Ile Malabar

The critical factor in assessing the likely distribution limits of N. aldafricanus on Ile Malabar is the distance to which habitat that is considered suitable extends east along the northern coast of the island. Various differences in the species composition of the mixed scrub vegetation of eastern and western Ile Malabar have already been described (Newbery and Hill 1981; Gibson and Phillipson 1983). A change occurs from the Gionnet type of mixed scrub to the more extensive Malabar type, but the details of the transitional zones were not known. Certain species of plants are exceptionally abundant in the NW of Aldabra ("northwestern species": Gibson and Phillipson 1983), and the frequencies of such species decline in the eastern region of Ile Malabar; we investigated this decline in 1983, using uncut transects marked on Fig. 1, to try and discover how mixed scrub suitable for the warbler graded into apparently unsuitable types.

Preliminary analysis of our results on the densities of plant species in the mixed scrub reveals that for a number of species there is a sharp decline in abundance in a particular section of the island: the Opark area. At this site there is an interruption of the coastal cliff, with a bay about 100 m wide which extends about 200 m inland before narrowing into a mangrove creek. As far as we could tell, this separates the mixed scrub belts along the northern coast on either side.

There are many differences in the density, architecture, and species composition of mixed scrub near Gionnet and Anse Petit Grabeau (Hambler et al. in prep.), but our most significant discovery is that some such differences are evident on opposite sides of Opark, despite the relatively short length of coastline involved. We illustrate this vegetation change in Table 2, in which selected species only are included; there are other plant species which do not follow the same trend, but we consider the species listed in the table are particularly useful in the context of a habitat change which might limit the warbler, and certain of these species are discussed in more detail in the following sections. The differences in vegetation across Opark, but particularly the dramatic decline in Dracaena reflexa and Tarenna supra-axillaris gave the very distinct impression that Gionnet-type mixed scrub ends at Opark.

It is probably not possible to determine how long there has been a difference in the vegetation on the opposite sides of Opark; the possibility that it is of recent origin cannot be excluded. We know of no studies of the vegetation in this area prior to our own in 1983. It is possible that the substrate is different west of Opark (which is an exceptional feature on the coastline), but a map of the geology of Aldabra (Braithwaite et al. 1973) does not suggest this; moreover, the topography of the Gionnet region is not thought peculiar (Thorpe and Stoddart 1969). We suggest that the vegetation differences across Opark may be partly the result of the activity of large herbivores, as discussed in Section II 2 d.

We now review individually features of the classic habitat, and its extent.

2) Review of features of the classic habitat

Although the combination of the four features listed in the Introduction is probably unique to Gionnet, it remains to be explained why this combination of features might be important to N. aldabranus whilst other unique habitats on Aldabra are apparently unsuitable.

a) Extremely dense, closed-canopy vegetation, with much litter and soil. "Dense" is a somewhat relative and ambiguous term in the context of vegetation, and is often used as a general description of the combined influences of rooted-plant density and architectural features such as abundance of twigs, leaves, etc.

The mixed scrub near Gionnet has been described as "dense tall scrub about 15 feet high, in places almost forest" (Fosberg in: Benson and Penny 1968), and as "extremely thick mixed scrub"... with exceptional "thickness of twigs and canopy right down to ground level" (Gibson and Phillipson 1983).

In 1983 we sampled mixed scrub on Ile Malabar, examining the densities of rooted woody plants, the height of the vegetation and the number of twigs of different sizes at various heights. The results of this study will be published elsewhere, but the general conclusion was that the scrub at Gionnet was not unique in its general density, but it is probably more consistently dense throughout the Gionnet region, with fewer of the more open areas found in mixed scrub elsewhere on Ile Malabar. There was a more obvious difference in the architecture of the mixed scrub near Gionnet than in the density of rooted plants: the abundance of D. reflexa and Pandanus spp. produced stands of vegetation which were locally extremely dense, as these plants have a rather different growth form to the other shrubs and trees (see illustrations in Fosberg and Renvoize 1980).

A rough relative measure of the density of the scrub is the ease with which it can be penetrated by people in a straight line without cutting. "Pemphis scrub" (Gibson and Phillipson 1983) is virtually impenetrable, and the bulk of the vegetation of Ile Malabar is Pemphis, which grades into mixed scrub along the northern part of the island. Using this measure, density increases inland away from the northern coast; we were able to penetrate an average of 225 m due south from the northern coast in the Gionnet Study Area, but 350 m in the Grabeau Study Area. In the Grabeau area and to the E the denser scrub is generally further inland. N. aldabranus does not appear to use the densest scrub (Pemphis).

The mixed scrub of Ile Malabar is heterogenous in many respects, and it is possible to find local areas with physical densities similar to that near Gionnet further east; the vegetation of Ile Polymnie is also very dense locally.

We sampled the height of the vegetation twice every 5 m of our transects for the first 100 m from the northern coast. The mean heights

and standard deviations for the Gionnet study area were: 0 to 50 m : mean 3.38 m, $s = 1.04$; 50 to 100 m : mean 2.77, $s = 1.02$. For the Grabeau area: 0 to 50 m : mean 1.90 m, $s = 1.67$; 50 to 100 m : mean 2.51 m, $s = 1.06$. This shows a highly significant ($p < 0.001$) decrease in the height of the mixed scrub over the first 100 m from the coast near Gionnet, and a significant ($p < 0.01$) increase in the same distance in the Grabeau area; for the full 100 m, Gionnet scrub is significantly taller than that near Grabeau ($p < 0.001$), but this is due to the difference in the most northerly section. These data suggest a habitat change inland, and to the east.

N. aldabranus may inhabit the most consistently dense and tall mixed scrub on Ile Malabar; Ile Polymnie appears rather similar, but requires study. Although this appears the least unusual feature of the classic habitat, it is worth noting that N. typica on Madagascar prefers thick vegetation (Milne-Edwards and Grandidier 1879; Rand 1936) although it is not confined to it (Benson 1960).

The depth of soil and leaf-litter at Gionnet is not unique on Ile Malabar (pers.obs.) but an unusual shallow organic type is present (Trudgill 1979), which may be important.

b) Large, dense stands of almost pure Pandanus tectorius. Pandanus stands were considered to be clearly associated with N. aldabranus from general observation of the birds (R.P. Prŷs-Jones, pers. comm.), and the plant is used as nest material and as a site for nesting (Benson and Penny 1968). However, the high use the warbler makes of Pandanus spp. at Gionnet may be purely facultative, and we believe there is insufficient evidence that the distribution of N. aldabranus is in any way related to the distribution of this plant. Prŷs-Jones (1979) presents some data suggested to support such an association, but we believe that the single quantitative measure that he uses (linear abundance) is not sensitive enough to give an accurate comparison of the amount of Pandanus at various sites. We found it impossible to quantify Pandanus abundance with any single measure, as the growth form of this large plant produces stands which differ considerably in height, shape, orientation and "solidness", reflecting the number of leaves and stems and the arrangement of stems.

Pandanus spp. would be available to N. aldabranus in the mid and eastern regions of Ile Malabar (and throughout much of Aldabra), but it is clear from journeys by boat along the northern coast of Ile Malabar that there is considerably more Pandanus in the western regions; the dominance by the species of the Gionnet vegetation has been noted by Gibson and Phillipson (1983) as exceptional. Some P. aldabrense was found near Gionnet in 1983 (F. Friedman, pers. comm.), but it is probably rare on Ile Malabar (C W.D. Gibson, pers. comm.).

A possible direct relationship between Pandanus and the warbler might be that the plant provides physical protection against predation of the nests by rats (Rattus rattus) (Prŷs-Jones 1979). We suggest a possible indirect importance of Pandanus in the habitat of N. aldabranus: the structure and height of these plants might provide some form of shelter on both a large scale in the Gionnet region, and on a

micro-environmental scale within the stands. This will be discussed further in Section II 3.

c) A high abundance of Dracaena reflexa

The particularly high abundance of D. reflexa was considered by Fosberg to be the only ecological peculiarity of the vegetation in which the warbler was first found (Benson and Penny 1968). The dominance of the Gionnet vegetation by this species (and by P. tectorius) is one of the characters Gibson and Phillipson (1983) note as exceptional compared with other Aldabra vegetation. D. McC. Newbery (pers. comm.) also considers the abundance of D. reflexa to be a particularly notable peculiarity of the classic habitat.

D. reflexa is generally uncommon on Aldabra; its distribution follows a "Northwest and Groves" restriction pattern (Gibson and Phillipson 1983). It is most abundant in Gionnet type mixed scrub, in which Gibson and Phillipson found it to be about ten times as frequent as in the vegetation in which it was next most abundant (Gionnet and Polymnie mixed Pemphis); Ile Polymnie mixed scrub is very similar to that at Gionnet, with the important exception that D. reflexa is far less abundant. Ile Picard has very local and limited stands of D. reflexa, and the Groves area of woodland on Grande Terre has a few plants of this species.

In our Gionnet study area we found that D. reflexa is common from the northern coast to at least 200 m inland, and is present more than 200 m inland here and W of Opark. It is noteworthy that the "Z" path, a transect which crosses Ile Malabar due south from the Gionnet region, is not representative in this respect, since it suggests the belt of high abundance of D. reflexa extends only 50 m inland from the coast (Prÿs-Jones, 1979: Appendix 2). This is an anomaly produced by the Anse Porché beach, behind which the path starts; this beach and bay occupy an area which would have been mixed scrub if the coastline had been straight; atypical plant species and human disturbance here are further complications. We found D. reflexa with high abundance, in thick stands, immediately W of Opark, and it is probable that it is present in similar quantity throughout the mixed scrub/mixed Pemphis between Opark and Passe Gionnet.

The northwestern distribution of D. reflexa (with certain other plants) may be explained by their sheltered position relative to the dry, salt-laden SW trade winds (Gibson and Phillipson 1983). The leaf surface of D. reflexa is not protected against high water loss (D. McC. Newbery, pers. comm.) and the species appears better adapted to the wetter parts of Aldabra. This will be discussed further in Section II 3.

N. aldabranus is known to spend considerable time foraging in stands of D. reflexa, although there is not sufficient evidence to demonstrate selective use of this plant (Prÿs-Jones 1979). We predict that detailed study would confirm such an association, since we predict certain invertebrates will favour the moist micro-environment this plant is likely to provide; this will also be expanded in Section II 3.

d) The absence of tortoises and goats

The Gionnet region, and Ile Polymnie, are unusual in that local

populations of the endemic giant tortoise and feral goats have recently been very low or absent (Bourn & Coe 1978; pers. obs.). These large herbivores may indirectly influence the distribution of N. aldabranus and so we present here evidence of population changes in these species which we suggest are of significance.

i. Numbers

Tortoises were reduced to very low numbers by exploitation before this century, and populations easily accessible from the settlement at Ile Picard were virtually exterminated; their numbers recovered rapidly this century when exploitation declined (Stoddart and Peake 1979). The population of tortoises on Ile Malabar was estimated to be about 2000 in the early 1970's (Bourn and Coe 1978), whilst there is not thought to be a population on Ile Polymnie (C.W.D. Gibson pers. comm.).

Goats were introduced to Aldabra before 1890, and their total population has suddenly increased alarmingly; in 1977 the total number was estimated to be 500 to 600 (Gould and Swingland 1980), but in 1982 it was estimated at 2560 + 560 (Newing et al. 1984). The population on Ile Malabar was estimated to be 200 to 250 in 1976 (Gould 1979), and that of Ile Malabar east of Anse Grande Grabeau was estimated to be 289 + 30 in 1982 (Newing et al. 1984). In 1983 we found fewer goats at the eastern end of Ile Malabar than in 1982, but more in the Anse Malabar/Anse Petit Grabeau area than in 1981. Given the distribution records below, these figures show a population increase and spread on Ile Malabar since 1976.

ii. Distribution

Tortoises were probably present throughout the length of Ile Malabar before their exploitation, and were probably particularly reduced in the more accessible western areas of the island. Fieldwork in 1972-74 suggested that tortoises were distributed in mixed scrub from the eastern tip of Ile Malabar to about 5 km E of Opark (Bourn and Coe 1978). Studies of goats between 1976 and 1977 suggested these also occurred over this range (Gould and Swingland 1980), i.e. up to Anse Petit Grabeau. No signs of goats or tortoises were found in brief explorations up to about 2 km W of Anse Petit Grabeau, nor near Anse Cédres Opark in 1975-76 (I.R. Swingland, pers. comm.). Brief visits to Opark between 1974 and 1977 revealed no signs of these animals (R.P. Prŷs-Jones 1979). Although Seychellois guides and workers think both goats and tortoises were present around Opark in the middle of this century (H. Charles, E. Constance and R. La Fontaine, pers. comm.), the numbers of large herbivores W of Anse Petit Grabeau must have been very low up to 1977.

In 1981 several goat and tortoise faeces were found about 1 km W of Anse Petit Grabeau (C.H., pers. obs.), and in 1983 we discovered goats and tortoises were present in numbers far too high to have been overlooked, up to the eastern bank of Opark. Tortoises were found throughout the Opark study area--i.e. up to 500 m W of Opark, but we could find no signs of goats W of Opark. The present western distribution limits of tortoises and goats are not clear, although we found no signs of them up to 2 km E of Gionnet. It is likely that there are more tortoises than goats W of Opark: the number of goats would have to be very low since no faecal pellets were found near the coast. There is an unconfirmed report that four tortoises were observed near Gionnet Camp in early 1983 (P. Bijoux,

pers. comm.). Our observations suggest very few large herbivores were present W of Opark in 1983.

It is clear that there has been a considerable increase in the numbers of both goats and tortoises in the western region of Ile Malabar, particularly E of Opark. This increase is likely to be a result of migration from more eastern regions, with continuous populations from Opark to Passe Houareau. In 1983 we found that three of the tortoises examined near Anse Cédres Opark had disk marks indicating they had moved from the Anse Malabar region (some 7 km away) since 1974 (Bourn and Coe 1978), and tortoises and goats were evident throughout the Grabeau study area in 1983. One tortoise nest was found near Anse Cédres Opark in 1983, but the smallest tortoises we found were about 10 to 15 years old--also suggesting movement was more important than reproduction in the population increase E of Opark.

Opark inlet is dry at low spring tides, and it is easy to cross on foot, small bays on each side providing points where access to and from the land surface is possible; the western bank is the more difficult to ascend and penetrate. The inlet may provide a relatively large obstacle to the movement of large herbivores on Ile Malabar, but there seems to be no absolute barrier, and it is possible that they could move round the inlet to the south. Although these herbivores may not favour the thick vegetation W of Opark, we believe it is only a matter of a few years before they cross the inlet in significant numbers.

iii. Impact

Tortoises and goats--the only large herbivores on Aldabra--may be responsible for some of the vegetation patterns on the atoll; however, the origins of most patterns are complex (Newbery and Hill 1981; Gibson and Phillipson 1983). It is useful to consider their potential impact on the habitat of N. aldabranus, by examining their distribution and behaviour in relation to the limits to the likely habitat of the warbler.

It is possible that the relative abundance of some plant species in the NW of Aldabra is related to the degree of exploitation of tortoises in these areas. However, enclosure experiments suggest that it is unlikely that release from grazing pressure alone would result in vegetation like that of Ile Polymnie (Gibson et al. 1983), nor like the similar Gionnet region.

In view of the dramatic vegetation differences across Opark, it is interesting to consider the known diets of the two herbivores. D. reflexa is a particularly important species to examine, as are other common species of the Gionnet mixed scrub which show a marked decline across the inlet.

Tortoises will readily eat D. reflexa (Grubb 1971) and are likely to damage it physically. However, they have not eliminated it on Ile Picard, or in the Groves, and are co-existing with it W of Opark (although they were found to be favouring stands of the species, judging by their faeces). Euphorbia pyrifolia and Tarenna spp. are considered unpalatable species for tortoises (Grubb 1971). It is thus unlikely that tortoises alone are responsible for the change across Opark.

Goats are capable of exploiting most vegetation types on Aldabra, and both graze and browse (pers.obs.). Although previously less dominant (Gould and Swingland 1980), goats are now having a striking impact on the vegetation of Aldabra, and on Grande Terre 36% of the scrub cover of some regions has been lost since 1978, particularly those species most palatable to goats (Newing et al. 1984). On eastern and middle Ile Malabar goats are now beginning to degrade vegetation (pers. obs. 1983). Goats are reported to take D. reflexa "more than occasionally" in studies of their food preferences on Ile Picard (Stevenson 1972); E. pyrifolia is a "preferred" food; Tarennia supra-axillaris and T. verdcourtiana, however, are not eaten at all frequently (but might be indirectly affected by scrub degradation).

It is probable that goats are involved in the vegetation change across Opark, but they cannot be considered entirely responsible, as some less palatable species show a decline across the creek, whilst some preferred food plants (such as Polysphaeria multiflora) did not decline greatly. It is likely that a "natural" decline in "northwestern" plant species on Ile Malabar has been exaggerated by goats.

We conclude this review of the likely significance of tortoises and goats to the distribution of N. aldabranus by suggesting that large herbivores may adversely modify the vegetation by selective removal of some plant species and by opening up the scrub cover; this may have restricted the range of N. aldabranus in the past. We suggest that the west/east decline in certain plant species across Opark and the decline in large herbivore numbers (particularly goats) in the reverse direction is not coincidental. The absence of large herbivores is probably a key feature of the classic habitat, but not the most important.

3) New hypotheses on the habitat of N. aldabranus

3.1) Other peculiarities of the Gionnet region

Although the Gionnet to Opark mixed scrub region appeared subjectively distinctive to us, it is hard to single out the characteristics which gave this impression. The four features reviewed above are each fairly obvious at Gionnet, but they do not provide sufficient information to explain the limits of the population of the warbler. Other areas on Aldabra possess combinations of these features, apparently without supporting warblers, and although it is possible the birds do not occupy all suitable habitats on Aldabra, it is instructive to consider other characteristics of the Gionnet region which add to its distinctiveness. These features will be labelled: e) and f).

e) Relatively high rainfall

A feature of the northwest of Aldabra that has recently been confirmed is that it receives a relatively high rainfall; several years of records from rain-gauges at up to 14 sites around Aldabra have been compiled by Stoddart (1983), and these are sufficient to detect some trans-atoll variations in rainfall in the study period (1973-1981) although some sites lack records in some years.

The NW of Aldabra generally receives a higher mean annual rainfall than the other regions of the atoll. In the NW, Anse Var (on Ile Picard) received the overall highest mean annual rainfall (1567 mm); Gionnet received the second highest (1448 mm) and the highest mean annual rainfall in three out of the seven years for which records are available (in 1976, 1979 and 1981); Anse Var received the highest mean annual rainfall in two of the four years for which records are available (in 1978 and 1980). The rainfall in the NW and at Gionnet is also relatively high in the driest six months of the year (June to November), and in this period Gionnet receives a consistently high rainfall-- no months with a mean rainfall of zero. The more easterly areas of Ile Malabar received a lower overall mean rainfall in the driest six months than did Gionnet and the NW (Stoddart 1983, figure 17).

Gionnet is probably not exceptional in its local rainfall, relative to the rest of the NW, but we consider the high rainfall it receives throughout the year to be an important link in the range of features which lead to the selective use of Gionnet by the warbler. Rainfall may be directly or indirectly important to N. aldabranus, particularly as in the dry season there is very little standing fresh water other than puddles after rain. Aldabra is relatively arid by comparison with other habitats used by Nesillas species, with the exception of N. typica lantzii of the subdesert in the SW of Madagascar. It is possible that Aldabra is a marginal habitat for Nesillas, in terms of water balance as in the dry season such a small island might provide fewer opportunities to acquire water (directly or in food) than do parts of the SW of Madagascar.

f) Relatively high species richness of the flora

The mixed scrub of Gionnet has a notably rich woody flora (D. McC. Newbery, pers. comm.; Gibson and Phillipson 1983). It is again not unique--the floras of Iles Picard and Polymnie are richer--but this may contribute to the quality of the habitat near Gionnet directly (e.g. through structural diversity) or indirectly (e.g. through herbivorous invertebrates see Frith 1979).

3.2) Synthesis of features of the classic habitat

We now combine the known features of the classic habitat ("a" to "f") with some predicted features ("g" and "h" below) to produce a general theory which may explain the restricted range of N. aldabranus on Aldabra.

We believe the most important and exceptional feature of the classic habitat is the high abundance of Dracaena reflexa. The distribution of this plant is not fully understood, and further examination of the substrate near Gionnet would be helpful. Substrate, available water and the activities of large herbivores may limit this plant's range on Aldabra; as this species is suspected to be susceptible to high transpirational water loss, we predict a likely feature of the Gionnet region:

g) Predicted micro-climate with high relative humidity and still air

We suggest that abundant D. reflexa will both depend on and produce a high relative humidity around the stands. This would be facilitated by a high and constant rainfall, a topographically sheltered position on the

atoll, and local windbreaks such as tall mangrove and Pandanus stands. Our subjective observations at Gionnet did suggest such a micro-climate, which might be important to the warbler in critical periods such as the dry season or when rearing young if standing water is less rapidly lost through evaporation. We predict a possible indirect importance of such a micro-climate:

h) Predicted high invertebrate food supply

Rainfall is probably related to the annual abundance and the types of insects on Aldabra (Cogan et al. 1971); local rainfall is almost certainly related to the local abundance of insects at various sites and times on the atoll (Frith 1979). Rainfall may act through increased humidity, and might act directly to increase invertebrate abundance and activity through decreased water-stresses, or indirectly e.g. through delaying leaf-fall. The classic habitat might provide diverse and numerous invertebrates for N. aldabranus, and this might be further increased by a rich flora (Frith 1979) and by the absence of strong winds. Spiders, winged ants and small moths are known to be eaten by N. aldabranus, at least occasionally in some numbers (Benson and Penny 1968). These invertebrates are not sufficiently known on Aldabra to test for an exceptional abundance near Gionnet; soil and litter arthropods do not appear exceptionally diverse or abundant near Gionnet (Spaul 1979), nor did those invertebrates sampled by Heath light traps (Frith 1979). However, neither of these surveys is comprehensive enough to support or refute our prediction: substrate is probably a major factor influencing ground-living invertebrates; the Heath trap is not a satisfactory sampling method for micro-lepidoptera (P.H. Sterling, pers. comm.) and many other groups; and Frith's trap at Gionnet was in "poor mixed scrub".

The invertebrates likely to be most significant to the warbler are those of the appropriate size range, active by day or sheltering by day in accessible places such as on bark or on leaves. We suggest the appropriate sampling method to test for feature "h" would be beating, and the dry season might be the most interesting time to compare the classic habitat with other areas. In passing, it is worth noting that there is a notorious abundance of mosquitos at Gionnet.

In concluding this synthesis, we suggest that it is significant that Nesillas warblers of the east and northwest of Madagascar "recherchent de préférence les endroits humides" (Milne-Edwards and Grandidier 1879). We suggest that features "a" to "h" could explain the limitation of a species of bird with very particular habitat requirements to the Gionnet to Opark mixed scrub, in addition this area of the atoll is, objectively, one of the most likely places to find a member of the genus Nesillas on Aldabra.

3.3) Predicted distribution of N. aldabranus

If we assume that the features of the classic habitat discussed above are in combination important to the warbler, we can predict the likely distribution limits to the current population. In general, we would predict that if N. aldabranus is present elsewhere on Aldabra, it is more likely to be in the mixed scrub in the NW--given the known (and probably related) vegetation and rainfall characteristics of that area.

The western limit to the population of the classic habitat appears to be Passe Gionnet (Prÿs-Jones 1979). This is a channel about 100 m wide, W of which the mixed scrub belt of the northern coast changes somewhat in character (Gibson and Phillipson 1983), probably reflecting a geological change (Braithwaite et al. 1973). Further W is the 600 m wide channel of Grande Passe, and west of this the mixed scrub is considerably different from that near Gionnet (Gibson and Phillipson 1983, and pers. obs.). Although there is considerably less D. reflexa on Ile Polymnie, we find it rather suprising that warblers have not been found there, and this island seems the most likely site for a population of the warbler outside Ile Malabar. It is possible that the absence of continuously abundant D. reflexa on Ile Polymnie breaks the vegetation into patches of suitable habitat too small to support a viable population of warblers. It is also possible that Passe Gionnet provides a barrier to voluntary movement of the warbler; it is notable that Nesillas is reported to fly poorly, and to be incapable of crossing "grands espaces d'une traite" (Milne-Edwards and Grandidier 1879).

The eastern limit of the Gionnet population seems less likely to be related to physical interruptions of the habitat; Opark inlet interrupts the mixed scrub, but Pemphis scrub behind it might permit movement round it. We suspect that a combination of the decline in rainfall to the E, and vegetation gradients, would have restricted the warbler to the western parts, and that the change across Opark marks the most likely eastern limit to the current population. Our limited sampling suggests that D. reflexa may decline slightly in abundance between Gionnet and the western bank of Opark (see Table 2), and it is likely that it declined gradually to the east of Opark before the encroachment of large herbivores. The nest found in 1983 gives hope that the warbler population does indeed reach Opark, but the probable record from near Anse Petit Grabeau in 1981 is too isolated to seriously suggest that the population extends this far east into such different vegetation.

Between Gionnet and Opark the mixed scrub belt is some 200 m wide; the species richness of the scrub, and the structural influence of Pandanus, decline inland from the northern coast. We find it surprising that N. aldabranus was not found more than about 50 m from the coast (Prÿs-Jones 1979, and pers. obs.), and it would be interesting both to search intensively for N. aldabranus in mixed scrub between Gionnet and Opark, and to examine micro-climatic gradients inland from the coast within the mixed scrub; there are patches of mixed scrub between 50 and 200 m from the coast which closely resemble the classic habitat in most features (other than Pandanus stands, few of which occur more than 100 m from the coast here), and these seem the most likely marginal habitat for the warbler.

The population of N. aldabranus was estimated to be under 25 individuals if suitable habitat extended 50 m inland and 9 km along the coast from Passe Gionnet (Prÿs-Jones 1979). We believe that in 1983 habitat that was closely similar to the classic one extended only to Opark, i.e. 4.5 km E from Passe Gionnet, and using the same assumptions for extrapolation the maximum likely population was about 13 individuals in 1983.

III. THE CONSERVATION OF N. ALDABRANUS

N. aldabranus is clearly endangered merely through its extremely limited distribution. It is not clear how long the population has been so small, but it is unlikely that a very small isolated population could survive long enough to become an endemic species with signs of island adaptations. It is probable that the warbler was either far more numerous and widespread on Aldabra in the past (perhaps in wetter periods of its history) or that the population is a relict of a recent colonisation by this species from an as yet undiscovered (and possibly extinct) population on another Indian Ocean island. If the former suggestion is correct we may now be witnessing the natural extinction of a species due to large-scale climatic and vegetation changes on Aldabra; long-term climatic changes are known to have occurred in the region (Stoddart and Walsh 1979; Walsh 1984) and standing fresh water has been more extensive on Aldabra in the past (Stoddart et al. 1971). In this case there is probably little that can be done to protect the species. If the population has always been restricted to a small area of Aldabra, or has been restricted at least in the last few centuries, then it is possible that Man might have indirectly influenced its abundance through the exploitation of tortoises and the introduction of goats and rats (Rattus rattus). It is possible that the warbler was able to colonise Aldabra, or temporarily flourished, because reductions in the populations of tortoises on certain islands of the atoll allowed vegetation similar to the classic habitat to expand. In the latter case, there would be more chance that the warbler could survive in the long term, provided reduction in its habitat through the encroachment of large herbivores can be prevented.

There is some recent evidence of vegetation changes in the Gionnet region since 1968: M.J. Penny (pers. comm.) reports that in 1984 he found that the areas of mixed scrub at both ends of Ile Malabar appeared less dense, with more dead twigs and branches, than expected. This would be worth investigating further. There is also evidence that the rat population is still widespread on Ile Malabar (we saw them frequently in all study areas in 1983) and there is evidence that their impact on Ile Malabar is increasing: we found rats had stripped bark from branches of 50 % of the Mystroxydon aethiopicum we examined, and a few Sideroxydon inerme bushes had also suffered damage. This stripping of bark was not apparent in the late 1970's (D.McC. Newbery, pers. comm.) nor in 1981 (pers. obs.). It is likely that rats will evolve to exploit the fauna and flora of Aldabra more seriously. Local control of rats might be possible in small areas (e.g. if a nest of the warbler were found in use) using new, highly specific poisons (I.R. Swingland, pers. comm.).

It is vital that the remaining habitat of N. aldabranus be monitored and protected. It seems likely that goats and tortoises would degrade the classic habitat; the control of goats is very urgent, and easier to justify than the control of the native tortoises. Although complete eradication of the goats would be extremely difficult (considering the history of failures in the attempts to eliminate them from other islands) it might be possible to achieve this ideal using extremely specific biological control agents such as viruses; this method was suggested to control mammalian pest species in the Galapagos (Swingland in Mitchell 1981). In the short-term, culling of goats in the Opark area, and towards

Passe Houareau, might reduce the rate at which they are spreading towards the west and the classic habitat of the warbler.

We suggest that human disturbance should be minimised between Passe Gionnet and Anse Malabar (to include the area of the 1981 record); any tourists visiting the Gionnet region should be careful to reduce the possibility that they may introduce exotic seeds or pests.

Positive measures to encourage the remaining population of N. aldabranus seem theoretically possible if our hypotheses are correct. It might be fairly easy to increase the availability of standing fresh water, using water-dispensing hoppers; this might be particularly worthwhile in the drier months. The food supply might be increased locally if barrels of water, with netting over the top, were provided before and during the breeding season. Such measures might influence other species, including potential predators and competitors of the warbler, and so would require very careful monitoring.

SUMMARY

No more than one individual of Nesillas aldabranus has been seen at a time in each observation of the species since 1976, and there is no proof that more than one survived in 1983 although some observations suggest that this was possible.

Records of ringed birds since 1977 include at least one seen in 1977, and three sightings of a bird, or birds, which had lost the colour ring but bore only the metal ring in September 1983. There were three sightings of the warbler in late 1983, in which the view was not good enough to see if rings were present; there were no observations of the species in 1984.

Sightings of ringed birds show one bird to have lived at least nine years by 1983.

All sightings of the species have been within the Gionnet coastal region of Aldabra Atoll. One probable record, which cannot be proven, as only the call was heard, was reported outside the classic habitat in the vicinity of Anse Petit Grabeau; this suggests it may be possible for the warbler to venture into habitat dissimilar to that at Gionnet. Exploration of the vegetation east of Gionnet revealed a very sharp decline in the abundance of certain plant species across the Opark inlet, most notably that in Dracaena reflexa. The likely extent of habitat considered suitable for a population of the warbler is thus re-defined to half its previously suggested length, so reducing the predicted maximum population of N. aldabranus to 13 individuals within the mixed scrub between Passe Gionnet and Opark. The extremely restricted range of the warbler is discussed; known, recently-confirmed and predicted features of the habitat of the species are united in a general theory which helps explain this range the abundance of Dracaena reflexa is considered the most ecologically atypical feature of the Gionnet region, and it is suggested to be no coincidence that the other exceptional feature of this region is that it is the only area of Aldabra which supports a warbler of the genus Nesillas.

The following hypotheses are presented which inter-relate the features of the habitat of the warbler and its restricted distribution:

i) Dracaena reflexa is a particularly important feature of the habitat of N. aldabranus.

ii) Relatively high rainfall and shelter from the trade winds favour D. reflexa at Gionnet; this plant may be restricted to the west of Gionnet by substrate changes, and to the east by large herbivores and lower rainfall.

iii) A combination of high rainfall and a particularly high degree of shelter from drying winds (due to location and tall vegetation) promote a high relative humidity in the micro-climate of the classic habitat, with the greatest humidity in and near stands of D. reflexa.

iv) High rainfall and a predicted high humidity are significant to the warbler for part or all of the year; these features may be important through the water requirements of the birds, or through the activity, abundance or species composition of their invertebrate food supply.

Large herbivores have spread at least 4 km west towards the habitat of the warbler since 1977. Goats are particularly likely to have degraded possibly suitable habitat, and will encroach into and degrade the habitat of the warbler unless urgently controlled. Rats still present a particularly great threat. Some positive conservation measures may be possible, and are required immediately if N. aldabranus is to be saved.

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REFERENCES

- Benson, C. W. 1960. Birds of the Comoro Islands. Ibis 103b: 5-106.
- Benson, C. W. and Penny, M. J. 1968. A new species of warbler from the Aldabra Atoll. Bull. Br. Orn. Club 88: 102-108.
- Bourn, D. and Coe, M. 1978. The size, structure and distribution of the giant tortoise population of Aldabra. Phil. Trans. R. Soc. Lond. B 282: 139-175.

- Braithwaite, C. J. R., Taylor, J. D. and Kennedy, W. J. 1973. The evolution of an atoll: The depositional and erosional history of Aldabra. Phil. Trans. R. Soc. Lond. B 266: 307-340.
- Cogan, B. H., Hutson, A. M. and Shaffer, J. C. 1971. Preliminary observations on the affinities and composition of the insect fauna of Aldabra. Phil. Trans. R. Soc. Lond. B 260: 315-325.
- Collar, N. J. and Stuart, S. N. 1985. Threatened birds of Africa and its related islands. The ICBP/IUCN Bird Red Data Book, Part I (3rd edition). Cambridge. ICBP/IUCN.
- Cowx, W. D. 1980. Final report vegetation transects SW Grande Terre. Report to Royal Society Aldabra Research Committee. (Unpublished.)
- Diamond, A. W. 1980. Seasonality, population structure and breeding ecology of the Seychelles brush warbler Acrocephalus sechellensis. Proc. 4th Pan-Afr. Orn. Congr., 253-266.
- Fosberg, F. R. and Renvoize, S. A. 1980. The flora of Aldabra and neighbouring islands. Kew Bull. addit. Ser. no 7. London, HMSO.
- Frith, D. W. 1979. A twelve month study of insect abundance and competition at various localities on Aldabra Atoll. Phil. Trans. R. Soc. Lond. B 286: 119-126.
- Gibson, C. W. D., Guilford, T. C., Hamblen, C. and Sterling, P. H. 1983. Transition matrix models and succession after release from grazing on Aldabra Atoll. Vegetatio 52: 151-159.
- Gibson, C. W. D. and Phillipson, J. 1983. The vegetation of Aldabra Atoll: preliminary analysis and explanation of the vegetation map. Phil. Trans. R. Soc. Lond. B 302: 201-235.
- Gould, M. S. 1979. The behavioural ecology of the feral goats of Aldabra Island. Ph. D. dissertation, Duke University, North Carolina, U.S.A.
- Gould, M. S. and Swingland, I. R. 1980. The tortoise and the goat: Interaction on Aldabra Island. Biol. Conserv. 17: 267-279.
- Grubb, P. 1971. The growth, ecology and population structures of giant tortoises on Aldabra. Phil. Trans. R. Soc. Lond. B 260: 327-372.
- Milne-Edwards, A. and Grandidier, A. 1879. Histoire physique, naturelle et politique de Madagascar, Volume XII, Histoire naturelle des oiseaux. Paris.
- Mitchell, A. W. 1981. Operation Drake: Voyage of discovery. London, Severn House Publishers Ltd.
- Newbery, D. McC. and Hill, M. G. 1981. Numerical description of "mixed scrub" vegetation on Aldabra Atoll. Atoll Res. Bull. 246: 1-13.

- Newing, T. J., Daly, K. H. and Hambler, K. 1984. Feral goats on Aldabra. Final report, Southampton University Expedition to Aldabra, 1982. Unpublished.
- Prÿs-Jones, R. P. 1979. The ecology and conservation of the Aldabra brush warbler Nesillas aldabranus. Phil. Trans. R. Soc. Lond. B 286: 211-224.
- Prÿs-Jones, R. P. and Diamond, A. W. 1984. Ecology of the land birds on the granitic and coralline islands of the Seychelles, with particular reference to Cousin Island and Aldabra Atoll. In: Stoddart, D. R. (ed). 1984. Biogeography and ecology of the Seychelles Islands. The Hague, Dr W. Junk Publishers.
- Rand, A. L. 1936. The distribution and habits of Madagascar birds. Bull. Amer. Mus. Nat. Hist. 72: 143-499.
- Spaul, V. W. 1979. Distribution of soil and litter arthropods on Aldabra Atoll. Phil. Trans. R. Soc. Lond. B 286: 109-117.
- Stevenson, J. A. 1972. A final report on feral goats, from Junior Staff Scientist to Scientific Co-ordinator. Aldabra Station Records. Unpublished.
- Stoddart, D. R. 1983. Spatial and temporal variability of rainfall on Aldabra Atoll. Atoll Res. Bull. 273: 223-246.
- Stoddart, D. R. and Peake, J. F. 1979. Historical records of Indian Ocean giant tortoise populations. Phil. Trans. R. Soc. Lond. B 286: 147-161.
- Stoddart, D. R. and Walsh, R. P. D. 1979. Long term climatic change in the western Indian Ocean. Phil. Trans. R. Soc. Lond. B 286: 11-23.
- Stoddart, D. R., Taylor, J. D., Fosberg, F. R. and Farrow, G. E. 1971. The geomorphology of Aldabra Atoll. Phil. Trans. R. Soc. Lond. B 260: 31-65.
- Thorpe, W. H. and Stoddart, D. R. 1969. The Aldabra warblers. New Sci. 41: 649.
- Trudgill, S.T. 1979. The soils of Aldabra. Phil. Trans. R. Soc. Lond. B 286: 67-77.
- Walsh, R. P. D. 1984. Climate of the Seychelles. In: Stoddart, D. R. (ed). 1984. Biogeography and ecology of the Seychelles Islands. The Hague, Dr W. Junk Publishers.

TABLE 1. CERTAIN AND POSSIBLE OBSERVATIONS OF NESILLAS ALDABRANUS 1977 - 1985. SEE TEXT FOR SOME DETAILS

<u>OBSERVER</u>	<u>DATE</u>	<u>LOCATION</u>	<u>CERTAINTY</u>	<u>NOTES ON OBSERVATION</u>	<u>REFERENCE</u>
C.W.D. GIBSON	1978	<u>Gionnet</u> : mixed scrub	certain	ringed bird seen, colour ring not seen	C.W.D. GIBSON pers. comm.
J.A. STEVENSON	Early 1981	<u>Gionnet</u> : 'A' path c. 200 m east of <u>Passe Gionnet</u>	v. probable	call heard, but bird not seen. (Several attempts to find birds by call-playback in 1980 - 1981.)	J.A. STEVENSON pers. comm.
C. HAMBLER & T.C. GUILFORD	1/9/1981	<u>Anse Petit Grabeau</u>	v. probable	distinctive call heard once	PERS. OBS.
G.Du CHATENET, H. CHARLES & K. GONSALVES	May/June 1983	<u>Gionnet</u> : 'A' path and mixed scrub	possible	calls heard whilst clearing 'W' path; possible v. brief view	H. CHARLES & K. GONSALVES pers. comm.
K. HAMBLER	1/9/1983	<u>Gionnet</u> : bank of <u>Passe Gionnet</u>	v. probable	3 calls heard in thick bush	PERS. OBS.
C. HAMBLER, K. HAMBLER & J.M. NEWING	2/9/1983	<u>Gionnet</u> : A28-A29	certain	1 bird seen and heard; ring on right leg, none on left	PERS. OBS.
C. HAMBLER	4/9/1983	<u>Gionnet</u> : A29	certain	bird as on 2/9/1983	PERS. OBS.
C. HAMBLER	6/9/1983	<u>Gionnet</u> : A27-A28	certain	bird as on 2/9/1983	PERS. OBS.
C. HAMBLER	16/9/1983	<u>Opark</u> : within 150 m only slight of western bank, c. possibility: 50 m inland	only slight possibility: nest only	old, fallen nest, with some similarities to nests of warbler: stored in British Museum, Tring with nests of <u>N. aldobranus</u>	PERS. OBS. AND SPECIMEN. SEE ALSO BENSON & PENNY (1968)
F.H. DRINKWATER	7/11/1983	<u>Gionnet</u> : 'A' path c. 500 m east of <u>Anse Porché</u>	almost certain	description of bird seen, and of call, matches the warbler, but no ring was seen and other (remote) possibilities exist; calls heard c. 100 m and a few mins. apart could be from 2 birds	F. DRINKWATER pers. comm.
F.H. DRINKWATER	18/11/1983	<u>Gionnet</u> : as on 7/11/1983	almost certain	bird as 7/11/1983 seen	F. DRINKWATER pers. comm.
F.H. DRINKWATER	20/11/1983	<u>Gionnet</u> : as on 7/11/1983	almost certain	seen as on 7/11/1983	" "
F.H. DRINKWATER	27/11/1983	<u>Gionnet</u> : as on 7/11/1983	v. probable	call heard	" "
F.H. DRINKWATER	8/12/1983	<u>Gionnet</u> : as above	almost certain	seen as on 7/11/1983	" "

TABLE 2

TABLE SHOWING THE NUMBER OF INDIVIDUALS OF SELECTED PLANT SPECIES IN VEGETATION TRANSECTS IN MIXED SCRUB ON ÎLE MALABAR.

The northernmost 100 m of the transects shown in Figure 1 are used in this table; each transect is 2 m wide. The origins of the transects are considered to be at random with respect to vegetation patterns within each study area. The species selected are the 15 most common species of woody plants found in these transects, plus Pandanus spp. These data are generally insufficient for statistical treatment, but are considered to illustrate patterns noted in our study.

'DIST.' denotes restriction of distribution (after Gibson and Phillipson 1983); the symbols used for distribution centres are: NW = northwest centred; G = groves; SE = southeast centred; P = P. acidula scrub.

'PAL.' denotes known palatabilities to large herbivores; the symbols used are: T = palatable to tortoises; G = palatable to goats; UT and UG denote unpalatability to tortoises and goats, respectively. Palatabilities are taken from Grubb (1971) for tortoises; and Stevenson (1982), Newing *et al.* (1984) and pers. obs. for goats.

SPECIES	DIST.	PAL.	STUDY AREA AND TRANSECT NUMBER (SEE FIGURE 1)													OPARK mean	ANSE PETIT GRABEAU				
			GIONNET			W. OPARK			E. OPARK			mean				10	11	12	13	14	mean
<u>Acalypha</u>			1	2	3	4	5	mean	6	7	mean	8	9	mean		22	11	12	34	37	23.2
<u>Claoxylodes</u>	NW, G	T, G	0	6	8	13	16	8.6	56	58	57.0	35	7	21.0							
<u>Apodytes</u>																					
<u>dimidiata</u>	SE	UT, UG	0	1	0	3	9	2.6	17	6	8.5	4	6	10.0		7	6	20	0	5	7.6
<u>Canthium</u>		, G	27	2	4	6	1	8.0	4	4	4.0	1	0	0.5		0	2	1	0	2	1.0
<u>bibracteum</u>																					
<u>Dicrostachys</u>		, G	2	1	3	16	20	8.4	8	3	5.5	0	0	0.0		0	0	0	0	0	0.0
<u>microcephala</u>	NW, G																				
<u>Dracaena</u>			80	48	71	54	27	56.0	44	8	26.0	0	0	0.0		0	0	0	0	0	0.0
<u>reflexa</u>	NW, G	T, G																			
<u>Euphorbia</u>			25	16	22	7	15	17.0	18	7	12.5	0	0	0.0		0	0	0	0	0	0.0
<u>pyrifolia</u>		UT, G																			
<u>Lomatophyllum</u>		UT, G	19	4	5	9	1	7.6	4	4	4.0	0	5	2.5		0	0	0	0	0	0.0
<u>aldabrense</u>																					
<u>Maytenus</u>			10	6	19	11	22	13.6	28	12	20.0	3	10	6.5		3	3	11	2	10	5.8
<u>senegalensis</u>		UT, G																			
<u>Myrtroxylon</u>			21	4	22	11	20	15.6	28	22	25.0	12	8	10.0		15	7	11	4	6	8.6
<u>aethiopicum</u>		UT, G																			
<u>Pemphis</u>			20	27	25	18	21	22.2	37	10	73.0	27	13	20.0		35	23	14	7	8	17.4
<u>acidula</u>		UT, G																			
<u>Polysphaeria</u>			94	15	41	41	48	47.8	93	32	66.0	59	34	46.5		29	12	50	14	19	24.8
<u>multiflora</u>		UT, G																			
<u>Sideroxylon</u>			4	2	11	14	13	8.8	5	6	5.5	2	3	2.5		10	0	1	0	2	2.6
<u>inermis</u>		UT, G																			
<u>Tarenna</u>			76	23	51	44	41	47.0	83	21	52.0	4	0	2.0		0	0	2	0	0	0.4
<u>supra-axillaris</u>	NW, G	UT, UG																			
<u>Tarenna</u>			12	3	8	10	4	7.4	34	13	23.5	3	2	2.5		1	0	3	0	2	1.2
<u>verdcourtiana</u>		UT, UG																			
<u>Terminalia</u>			6	2	4	5	4	4.2	1	5	3.0	3	0	1.5		2	0	0	0	1	0.6
<u>boivinii</u>		T, G																			
<u>Pandanus</u> spp.		,	2	1	3	0	0	1.2	0	1	0.5	0	0	0.0		0	0	4	0	0	0.8

ATOLL RESEARCH BULLETIN

No. 291

CHANGES IN THE DISTRIBUTION OF THE COCCID
ICERYA SEYCHELLARUM WESTW. ON ALDABRA ATOLL
IN RELATION TO VEGETATION DENSITY

By

D. McC. NEWBERY AND M. G. HILL

ISSUED BY

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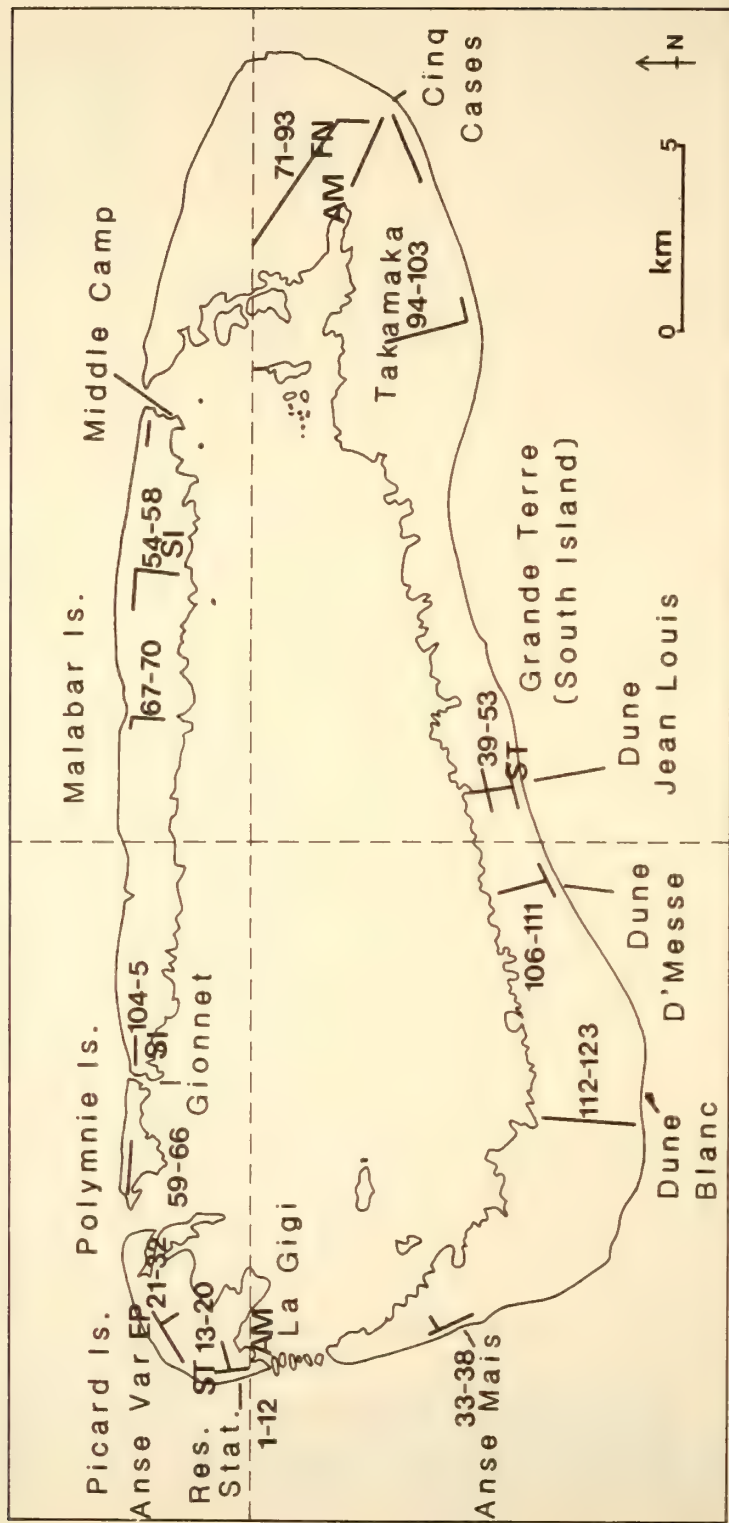


Fig. 1. Aldabra Atoll showing the areas sampled in the 1983 resurvey and the locations of monitoring sites for the species: AM, *Avicennia marina*, EP, *Euphorbia pyrifolia*, FN, *Ficus nautarum*, SI, *Sideroxylon inerme*, ST, *Scaevola taccada*. Numbers refer to the number of sampling points.

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By

D. McC. NEWBERY¹ AND M. G. HILL²

ABSTRACT

1. The overall abundance of Icerya seychellarum Westw. (Margarodidae : Homoptera), on Aldabra Atoll in the Western Indian Ocean, has changed little between 1978 and 1983 but its spatial distribution over the atoll has altered markedly. 2. Several susceptible host tree species showed ten-fold or more higher median infestation levels in the SE than the NW quadrant of the atoll. These differences were not evident in 1978. 3. The results of the 1983 survey are supported by biannual monitoring of five species of host trees from 1980 to 1983. 4. Since 1978 the level of coccid infestation has risen in the SE, where tree mortality is largely density independent, but has remained low in the NW, where tree mortality is more density dependent.

Keywords: Coccids Aldabra Atoll Distribution Hosts Vegetation Density.

INTRODUCTION

Two surveys of the distribution of the coccid, Icerya seychellarum, Westw. (Margarodidae : Homoptera), in 1976/77 and in 1978 on Aldabra Atoll, showed an overall low abundance (Hill and Newbery, 1980) compared with the peak infestations of 1975 (Renvoize, 1975). Host tree species differed considerably in their susceptibility to coccids (Hill and Newbery, 1980; Newbery, Hill and Waterman, 1983) but the abundance of coccids on any host species varied insignificantly between different areas of the atoll. Thus, by late 1978, the outbreak which had started c. 1968 (Hill and Newbery, 1982) appeared to have settled down to an even and residual level. In this paper we report the results of a re-survey of the status of I. seychellarum on Aldabra in 1983 and monitoring of the coccid on five tree species between 1980 and 1983.

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METHODS

Survey of coccid distribution and abundance

Between July and August 1983, we recorded the abundance of I. seychellarum on the woody flora of Aldabra in the areas shown in Figure 1. Apart from the recently-opened long transect in the south-west, these areas were approximately the same as those sampled in the 1976/77 and 1978 surveys by Hill and Newbery (1980).

The woodlands and shrub vegetation were sampled by a plotless method. In each area sampling points were chosen either in a pseudo-random, representative manner, or evenly at intervals of c. 100m along transect lines. At each sampling point the nearest thirty trees were identified and the coccid infestation scored as a composite value for each individual tree and on the same scale used in 1976/77 and 1978, viz: 0, no coccids found after searching; 1, few coccids found after searching; 2, numerous coccids evident without searching; 3, vast numbers of coccids; 4, coccid infestation devastating. Our hundred and twenty-three sampling points were all in 'mixed-scrub' vegetation (Newbery and Hill, 1981; Gibson and Phillipson, 1983) and these were supplemented by observations on all individuals of susceptible species when encountered in walking between sampling points. In this context a susceptible species was one which had a median infestation score of 1.0 or more in the 1976/77 or 1978 surveys. Mangrove, Pemphis acidula-dominated, and coastal scrub communities were sampled in a similar but less intensive manner. (Authorities for plant species are included in Table 1.) Time was not available to comprehensively search for rare tree species.

The results of the late 1983 monitoring (referred to below) were added to our sample. Excluding seven uncommon host-tree species, each of which had less than ten individuals, 5137 trees and woody shrubs were sampled from thirty-six species.

Monitoring

In the light of the earlier surveys (Hill and Newbery, 1980) and detailed studies on highly susceptible species (Newbery, 1980a,b,c and Hill, 1980), thirty individuals of each of five heavily infested tree species were randomly selected and tagged along transects in areas of the atoll where they were locally abundant and highly infested in 1980 : Scaevola sericea (near the Research Station, Picard Island, and near Dune Jean Louis, Grande Terre); Euphorbia pyrifolia (Anse Var, Picard Island); Ficus nautarum (Cinq Cases, Grande Terre); Sideroxylon inerme (Gionnet and Middle Camps, Malabar Island) and Avicennia marina (La Gigi, Picard Island, and Cinq Cases creek, Grande Terre).

Trees were scored for coccid abundance biannually from 1980 to 1983 using the survey scoring scale of 0 to 4. Where an individual tree died between the sampling times the number of replicates were fewer at the time of measurement and these numbers were made up by

randomly selecting and tagging new individuals. (*E. pyrifolia* was not sampled in the first six months of 1980: In one case, *S. sericea* near Dune Jean Louis, the number of replicate bushes was twenty-three; and in twelve other of the sixty-four species-site-time combinations this number was between twenty-six and twenty-nine.)

RESULTS

Comparison with previous surveys

The median infestation scores of the thirty-six species are shown in Table 1 for the whole atoll and for its four quadrants (Fig. 1). Thirty-two species had median infestation scores greater than nil in either the 1983 survey or one of the 1976/77 or 1978 surveys (Table 1, Hill and Newbery, 1980). Spearman rank correlations between the scores in 1983 and scores in 1976/77, and in 1978, were highly significant ($P < 0.01$, $r = 0.773$ and 0.864 respectively), indicating that those species which were highly and lowly infested in 1976/77 and 1978 remained so in 1983.

For the whole atoll the changes in median infestation for these thirty-two species between 1976/77 and 1983 and between 1978 and 1983 were not significant by sign tests (15+, 17- ; 18+, 10- , 4 nil differences respectively, $P > 0.05$). Of the ten most heavily infested species in 1983 (Table 1), between 1976/77 and 1983 five increased and five decreased in infestation and the same occurred between 1978 and 1983.

Variation in infestation across the atoll (1983)

Ficus nautarum, *Sideroxylon inerme* and *Apodytes dimidiata* show approximately ten-fold higher mean infestation scores in the SE quadrant than in the NW quadrant, and *Avicennia marina* shows a sixteen-fold difference in the same direction. For *Pemphis acidula* the infestation in the SE is about sixty times that in the NW, though it must be noted that this is coastal and mixed-scrub *P. acidula* and not the main *P. acidula* dominated vegetation zone in which individuals are rarely infested. *Scaevola sericea* and *Polysphaeria multiflora* differed little in infestation between the SE and NW quadrants : many other species in Table 1 had either sample sizes that were too small for analysis or median infestations that were too low to make comparisons across the atoll. The NE, like the NW, quadrant had comparatively low infestation scores, even on the generally more susceptible species; but in the SW quadrant (most of which was not accessible for sampling in 1976/77 and 1978) *Sideroxylon inerme*, *Scaevola sericea* and *Polysphaeria multiflora* had notably high and similar levels of infestation to those the SE quadrant.

Clearly, in the SE quadrant the susceptible host species support higher median infestation levels than in the NW quadrant with the SW and NE quadrants being intermediate. Comparing the median infestation scores in the NW quadrant (1983) with those over the whole atoll in

1976/77, and in 1978, shows no significant change ($P > 0.05$) by sign tests (8+, 9-, 2 nil ; 7+, 11-, 1 nil differences, respectively). Similarly, for the SE quadrant the sign tests show an overall rise, but this is significant at only $P \leq 0.1$ (10+, 4-, 1 nil differences in both cases).

Differences in weighted abundance of coccids across the atoll

In 1976/77 Newbery and Hill (1981) recorded the percentage cover abundance of trees and woody shrubs in sixty-five, mostly 20 x 20 m plots, during the course of that coccid survey. The 1983 coccid data were collected from the same areas (comparing Fig. 1 in Hill and Newbery, 1980 with Fig. 1 here) and there has been little visible change in the vegetation and its composition in that time interval (excepting unusually damaged vegetation inland of Dune Jean Louis - Newbery personal observation 1983). Those vegetation data may be used to calculate weighted vegetation coccid scores for the 'mixed-scrub' areas in the NW and SE quadrants. The NE was less intensively sampled for coccids, both earlier and in 1983, and the flora of the SW has, in its widest part, only been recently investigated (C. Peet and D. Cowx unpublished) and not with comparable plot records. The thirty-three commonest species were used : fourteen rarer (less than 1% cover) and very infrequently infested species were excluded. The mean percentage cover abundance for each species was calculated for thirteen NW quadrant plots and twenty-eight SE quadrant plots. (Of these latter, one was of coastal Scaevola sericea dominated scrub and two others lay in the Thepesia populneoides - Lumnitzera racemosa association inland of Cinq Cases creek). The coccid score for each host species in the two quadrants was weighted by the hosts' mean cover abundance and the overall weighted mean found. For the NW quadrant this mean (still on the 0 to 4 coccid scoring scale) was 0.120 and in the SE quadrant was 0.363 - a three-fold difference across the atoll.

Changes in infestation over four years

Coccid infestations on monitored tree species generally continued to decline on Aldabra between 1980 and 1983, except for the SE monitored Avicennia marina and Ficus nautarum (Fig. 2) which appeared to increase. Infestations have been high on Scaevola sericea, Avicennia marina and Ficus nautarum to a similar level shown in the 1976/77, 1978 and 1983 surveys. The most obvious decline from moderate infestations in 1980 to near zero levels in 1983 were for Sideroxylon inerme (Malabar Island) and Avicennia marina (Picard Island).

DISCUSSION

The two previous surveys of 1976/77 and 1978 were conducted in Aldabra's wet season whilst access to the atoll was only possible at the end of the wet season and the start of the dry season in 1983. It is unlikely that differences between the 1983 and previous results were due to meteorological changes because, apart from species like

Euphorbia pyrifolia which are deciduous (Newbery, 1980b), phenology was not a significant factor in host tree susceptibility (Newbery, Hill and Waterman, 1983) and monitoring over the four years (Fig. 2) did not show periodic changes in infestation levels from dry to wet season. Overall, there has been little qualitative change (in the terms of numbers of host species increasing and decreasing) in the status of I. seychellarum on Aldabra between 1976 and 1983, and this is supported by the monitoring results. Within the atoll there have developed marked differences between the NW and SE quadrants with indications of serious local increases in the SE between 1976 and 1983.

Aldabra has become drier in recent years. Stoddart (1984) has analysed eight years of atoll rainfall patterns based on a rain-gauge circuit of thirteen stations around the atoll (1974-1981). Grouping the yearly total rainfall results for stations within each of the four quadrants (and excluding that for Ile Esprit) for the years 1976 to 1981, the NW quadrant decreased by 41% from 1695 mm to 999 mm. Similarly, for the NE, SE and SW quadrants respectively the changes were: 1209 to 798 (34%); 1229 to 856 (30%); and 1273 to 855 (33%). The SE is consistently drier than the NW, though suffered a slightly smaller decrease in rainfall than the NW between 1976 and 1981.

It seems unlikely that the infestation in the NW was lower because an agent of biological control has taken effect in these recent years. In 1983 no coccinellid beetles were seen and in 1976-1978 Hill and Blackmore (1980) found only a few beetles after searching. Parasites were not found in 1976-1978 and in 1983 there was no evidence of dead colonies which could have been a result of these or of a pathogen.

There are large differences in habitat between the NW and SE quadrants of the atoll. In geomorphology, the NW has a rough, dissected terrain of pavé and champignon coral whilst in the SE the predominant form is flat plain limestone (Stoddart et al., 1971) except for the areas just inland of the south coast. As a consequence soils fill wide shallow basins in the SE whereas in the NE trees are rooted in much smaller, often deeper pockets (Trudgill, 1979a,b). The vegetation in the NW is a species-rich closed canopy (average percentage cover of woody species 131%, Newbery and Hill, 1981) compared with the relatively species-poor and more open (85% cover) canopy in the SW (see also Hnatiuk and Merton, 1979a,b and Gibson and Phillipson, 1983). The vegetation in the SE is more exposed than in the NW to SE trade winds during the dry season (Hnatiuk, 1979). These factors suggest that decreased rainfall will be more deleterious to the vegetation in the SE than in the NW, and greater water stress may, in part, explain the higher levels of coccid infestation in the SE (Newbery, 1980a,c).

Against this hypothesis is the observation that the mangrove Avicennia marina will not be short of water in dry season yet this species shows one of the greatest differences in infestation between the NW and SE quadrants. Newbery (1980a) has suggested that one of the controlling factors of infestation on A. marina is the build-up of excreted salt on the younger leaves and therefore frequent rain

may keep leaves more receptive to coccid settlement. Possibly increased immigration onto A. marina from other stressed plants led to high levels in the SE.

An alternative, but not isolated, hypothesis follows from Hill and Newbery (1980). The peak infestation levels in 1975 (Renvoize, 1975) were at levels far greater than those we recorded in 1976/77 and 1978 and may have caused the death of some susceptible trees (Newbery 1980b,c). These deaths would have thinned the vegetation and left young, more resilient, individuals. Could this have happened faster in the NW than in the SE? In the SE the trees are more widely spaced and mortality is probably density independent in the main due to environmental factors (Stoddart and Wright, 1967) and to grazing (feral goats, Gould, 1979; and tortoises, Merton, Bourn and Hnatiuk, 1976) which predominates in the SE. In contrast, tree mortality in the denser luxuriant vegetation of the NW is likely to be more density dependent.

In the NW there is ample evidence of tree regeneration (Newbery pers. obs.), whereas in the SE the grazers reduce seedling survival and hence regeneration, especially in the areas where grazers and coccids are both abundant. Removal of phloem sap by coccids in dense vegetation will mean that an infested, and therefore weakened, tree (Newbery 1980b,c) is less able to compete with its non-infested neighbours and would be rapidly thinned from the vegetation. Where there is sufficient rainfall, trees could maintain a rapid leaf turnover rate leading to high rates of leaf mortality for a sedentary stylet feeder such as I. seychellarum, (Hill, 1980). Conversely, in the SE the same species, less affected by tree-tree competition, although debilitated by coccids, would be expected to survive longer and to either have a slower leaf turnover rate or become deciduous as a result of the drier environment.

Evidence from several species supports this role of vegetation density in the population regulation of I. seychellarum:

1. The highly infested fig trees (Ficus nautarum) in the SE are large, imposing trees whilst in the NW they tend to be smaller, growing in amongst other shrub and tree species. Similarly, the heavily infested Guettarda speciosa trees in the SE are well separated from neighbours and therefore probably suffer less competition as a result. Apodytes dimidiata, commonly infested in the SE, does grow in small clumps of trees and shrubs though not infrequently as separated individuals. Lastly, Avicennia marina stands sampled at La Gigi, Picard Island (Newbery, 1980a) and at Cinq Case creek are structurally different: The NW site shows colonization on a sand bar with young growth and competition, whereas the trees in the SE are larger and more spaced in coral pockets at the upper limit of the tide and where the zone of brackish pools begins.

2. Species such as Scaevola sericea that tend to grow as monospecific stands of similar density in the NW and SE, suffer intraspecific competition between similarly infested individuals and showed little difference in infestation levels between these quadrants (Table 1).

Polysphaeria multiflora is a small tree species of dense mixed-scrub and woodland over most of the atoll (Newbery and Hill, 1981; Gibson and Phillipson, 1983) and, rarely being found as an isolated individual, also showed similar infestation levels in the NW and SE.

3. Lumnitzera racemosa and Thespesia populneoides do not afford a NW - SE comparison as they form a special community type only in the SE. Calophyllum inophyllum dominates an isolated grove in the SE, and Casuarina equisetifolia occurs in the NW and NE. However, for T. populneoides (much less so L. racemosa which lines brackish pools), it was common to find well spaced individuals which were frequently heavily infested (Table 1).

4. Pemphis acidula mainly occurs as an almost monospecific band of vegetation around the atoll inland of the lagoon mangroves (Gibson and Phillipson, 1983), and there it is very lightly infested. In the sparser vegetation along the SE coast it had moderate infestation levels. Sideroxylon inerme provides an interesting case, because it also had higher infestation levels in the SE than in the NW. In the NW this species is commonly found in either dense P. acidula stands or in mixed-scrub, whereas in the SE it occurs as isolated trees.

Our findings and hypothesis illustrate an important ecological principle. This new immigrant insect to the island ecosystem of Aldabra is still settling into its fundamental niche (MacArthur & Wilson, 1967; Pianka, 1978). The extent to which this niche is developed differs in different vegetation types. In the parts of the atoll (NW) where the vegetation appears to be near equilibrium we suggest that the original outbreak has been dampened to a residual level by a process of negative feedback (thinning and the capacity for vegetation regrowth) whereas in the non-equilibrium parts (SE) which are subject to stronger environmental stresses enforcing the effects of increasing large herbivore pressures on the vegetation, a recent positive feedback has occurred in the form of a small upward oscillation in coccid abundance. On this basis, we predict that coccid abundance will fall back to a residual level in the SE once the susceptible host trees have all died out. And, since the regeneration of these host species is limited in the SE, this residual level may well be lower than that in NW, not precluding the possibility that in a few decades present young individuals of susceptible species will have aged and become more infested in the NW.

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REFERENCES

- Gibson, C. W. D. & Phillipson, J. (1983). The vegetation of Aldabra Atoll : preliminary analysis and explanation of the vegetation map. Philosophical Transactions of the Royal Society of London, B, 302, 201-235.
- Gould, M. S. (1979). The Behaviour ecology of the feral goats of Aldabra Island. PhD Thesis. Department of Zoology, Duke University.
- Hill, M. G. (1980). Susceptibility of Scaevola taccada (Gaertn.) Roxb. bushes to attack by the coccid Icerya seychellarum. Westwood: the effects of leaf loss. Ecological Entomology, 5, 345-352.
- Hill, M. G. & Blackmore, P. J. M. (1980). Interactions between ants and the coccid Icerya seychellarum on Aldabra Atoll. Oecologia (Berlin), 45, 360-365.
- Hill, M. G. & Newbery, D. McC. (1980). The distribution and abundance of the coccid Icerya seychellarum. Westw. on Aldabra Atoll. Ecological Entomology, 5, 115-122.
- Hill, M. G. & Newbery, D. McC. (1982). An analysis of the origins and affinities of the coccid fauna (Coccoidea : Homoptera) of Western Indian Ocean islands with special reference to Aldabra Atoll. Journal of Biogeography, 9, 223-229.
- Hnatiuk, R. J. (1979). Temporal and spatial variations in precipitation on Aldabra. Philosophical Transactions of the Royal Society of London, B, 286, 25-34.
- Hnatiuk, R. J. & Merton, L. F. H. (1979). A perspective of the vegetation of Aldabra. Philosophical Transactions of the Royal Society of London, B, 286, 79-84.
- Hnatiuk, R. J. & Merton, L. F. H. (1979). The vegetation of Aldabra : a reassessment. Atoll Research Bulletin, 239: 1-22.
- MacArthur, R.H. & Wilson, E.O. (1967) The Theory of Island Biogeography. Princeton University Press, New Jersey.
- Merton, L. F. H., Bourn, D. M. & Hnatiuk, R. J. (1976). Giant tortoise and vegetation interactions on Aldabra Atoll - Part 1 : Inland. Biological Conservation, 9, 293-304.
- Newbery, D. McC. (1980a). Infestation of one coccid, Icerya seychellarum (Westw.), on the mangrove Avicennia marina (Forsk.) Vierh. on Aldabra Atoll, with special reference to tree age. Oecologia (Berlin), 45, 325-330.
- Newbery, D. McC. (1980b). Interactions between the coccid, Icerya seychellarum (Westw.), and its host tree species on Aldabra Atoll. I. Euphorbia pyrifolia Lam. Oecologia (Berlin), 46, 171-179.
- Newbery, D. McC. (1980c). Interactions between the coccid, Icerya seychellarum (Westw.), and its host tree species on Aldabra Atoll. II.

- Scaevola taccada (Gaertn.) Roxb. Oecologia (Berlin), 46, 180-185.
- Newbery, D. McC. & Hill, M. G. (1981). Numerical classification of 'mixed-scrub' vegetation on Aldabra Atoll. Atoll Research Bulletin, 246:1-13.
- Newbery, D. McC., Hill, M. G. & Waterman, P. G. (1983). Host-tree susceptibility to the coccid Icerya seychellarum Westw. (Margarodidae : Homoptera) on Aldabra Atoll : the role of leaf morphology, chemistry and phenology. Oecologia (Berlin), 60, 333-339.
- Pianka, E. R. (1978). Evolutionary Ecology. 2nd ed. Harper & Row, New York.
- Renvoize, S. A. (1975). Icerya seychellarum on Aldabra. Unpublished Royal Society Aldabra Research Station Report, ALD/21(75), 41pp.
- Stoddart, D. R. (1984). Spatial and temporal variability of rainfall on Aldabra Atoll. Atoll Research Bulletin (in press).
- Stoddart, D. R., Taylor, J. D., Fosberg, F. R. & Farrow, G. E. (1971). Geomorphology of Aldabra Atoll. Philosophical Transactions of the Royal Society of London, B, 260, 31-65.
- Stoddart, D. R. & Wright, C. H. (1967). Geography and ecology of Aldabra atoll. Atoll Research Bulletin, 118, 11-52.
- Trudgill, S. T. (1979a). Surface lowering and landform evolution on Aldabra. Philosophical Transactions of the Royal Society of London, B, 286, 35-45.
- Trudgill, S. T. (1979b). The soils of Aldabra. Philosophical Transactions of the Royal Society of London, B, 286, 67-77.

Table 1 Median infestation scores of Icerya seychellarum on the tree flora of Aldabra Atoll in 1983. (n is the sample size)

	NW			SW			QUADRANT			SE			WHOLE ATOLL
	n	n	n	n	n	n	NE	n	n	n	n	n	
<u>Lumnitzera racemosa</u> Willd. var. <u>racemosa</u>	--	0	--	--	0	--	--	0	2.41	59	2.41	59	
<u>Thespesia populneoides</u> (Roxb.) Kostel.	--	1	--	--	0	--	--	0	1.85	169	1.85	170	
<u>Ficus nautarum</u> Baker	0.32	18	--	--	3	0.06	--	19	3.00	58	1.65	98	
<u>Avicennia marina</u> (Forsk.) Vierh.	0.11	29	--	--	0	--	--	0	1.61	59	1.06	88	
<u>Allophylus aldabricus</u> Radlk.	0.97	50	--	--	2	--	--	0	--	3	1.03	55	
<u>Casuarina equisetifolia</u> L.	1.13	94	--	--	0	0.92	--	66	--	0	1.03	160	
<u>Sideroxylon inerme</u> L. ssp. <u>cryptophlebica</u> (Baker) Hemsley	0.25	145	1.68	215	0.54	116	2.50	17	0.90	121	0.74	200	
<u>Scaevola sericea</u> Vahl	0.72	46	2.50	8	0.04	25	0.90	121	0.70	14	0.70	14	
<u>Calophyllum inophyllum</u> L. var. <u>takamaka</u> Fosb.	--	0	--	--	0	--	--	0	0.70	14	0.70	14	
<u>Guettarda speciosa</u> L.	--	0	0.73	68	--	4	1.17	116	0.68	188	0.68	188	
<u>Euphorbia pyrifolia</u> Lam.	0.59	51	--	3	--	0	0.00	8	0.50	62	0.50	62	
<u>Ficus reflexa</u> Thunb.	0.83	14	--	1	0.23	16	--	1	0.44	32	0.44	32	
<u>Azima tetracantha</u> Lam.	0.50	31	0.07	8	--	5	--	2	0.38	46	0.38	46	
<u>Dichrostachys microcephala</u> Renvoize	0.38	42	--	0	--	0	--	0	0.38	42	0.38	42	
<u>Polysphaeria multiflora</u> Hiern.	0.31	210	0.62	226	0.00	70	0.44	345	0.36	851	0.36	851	
<u>Ficus avi-avi</u> Bl.	0.50	8	--	2	0.30	34	--	0	0.35	44	0.35	44	
<u>Pemphis acidula</u> Forst.	0.02	22	--	5	0.00	8	1.21	38	0.27	73	0.27	73	
<u>Apodytes dimidiata</u> E. Mey. ex Arn.	0.04	39	0.04	71	0.06	20	0.40	267	0.24	397	0.24	397	
<u>Maytenus senegalensis</u> (Lam.) Exell	0.02	106	0.03	110	--	2	0.01	163	0.18	381	0.18	381	
<u>Erythroxylon acranthum</u> Hemsf.	0.11	22	--	1	--	3	--	5	0.08	31	0.08	31	
<u>Clerodendrum glabrum</u> E. Mey.	0.00	10	--	5	--	0	--	3	0.06	18	0.06	18	
var. <u>minutiflorum</u> (Bak.) Fosb.													
<u>Flacourtia ramontchii</u> L'Hér.	0.00	12	0.05	32	--	3	0.07	42	0.04	89	0.04	89	
var. <u>renvoizei</u> Fosb.													
<u>Tarennia tricantha</u> (Bak.) Brem.	0.04	26	0.00	16	0.00	8	0.03	54	0.02	104	0.02	104	

Footing to Table 1.

Species with infestation of 0.01 (n) : Dracaena reflexa Lam. var. angustifolia Baker (42), Jasminum elegans Knobl. (36), Mystroxydon aethiopicum (Thunb.) Loes (398), Tricalysia sonderana Hiern. (68), Tarenna supra-axillaris (Hemsl.) Bremek (168).

Species with infestation of 0.00 : Acalypha claoxylodes Hutch. (91) Brong. (33) Canthum bibracteatum (Bak.) Hiern. (93), Colubrina asiatica (L.) Brong. (33), Cordia subcordata Lam. (14), Ochna ciliaris Lam. (373), Tournefortia argentea L.f. (15), Terminalia boivinii Tul. (71), Tarenna verdcourtiana Fosb. (40).

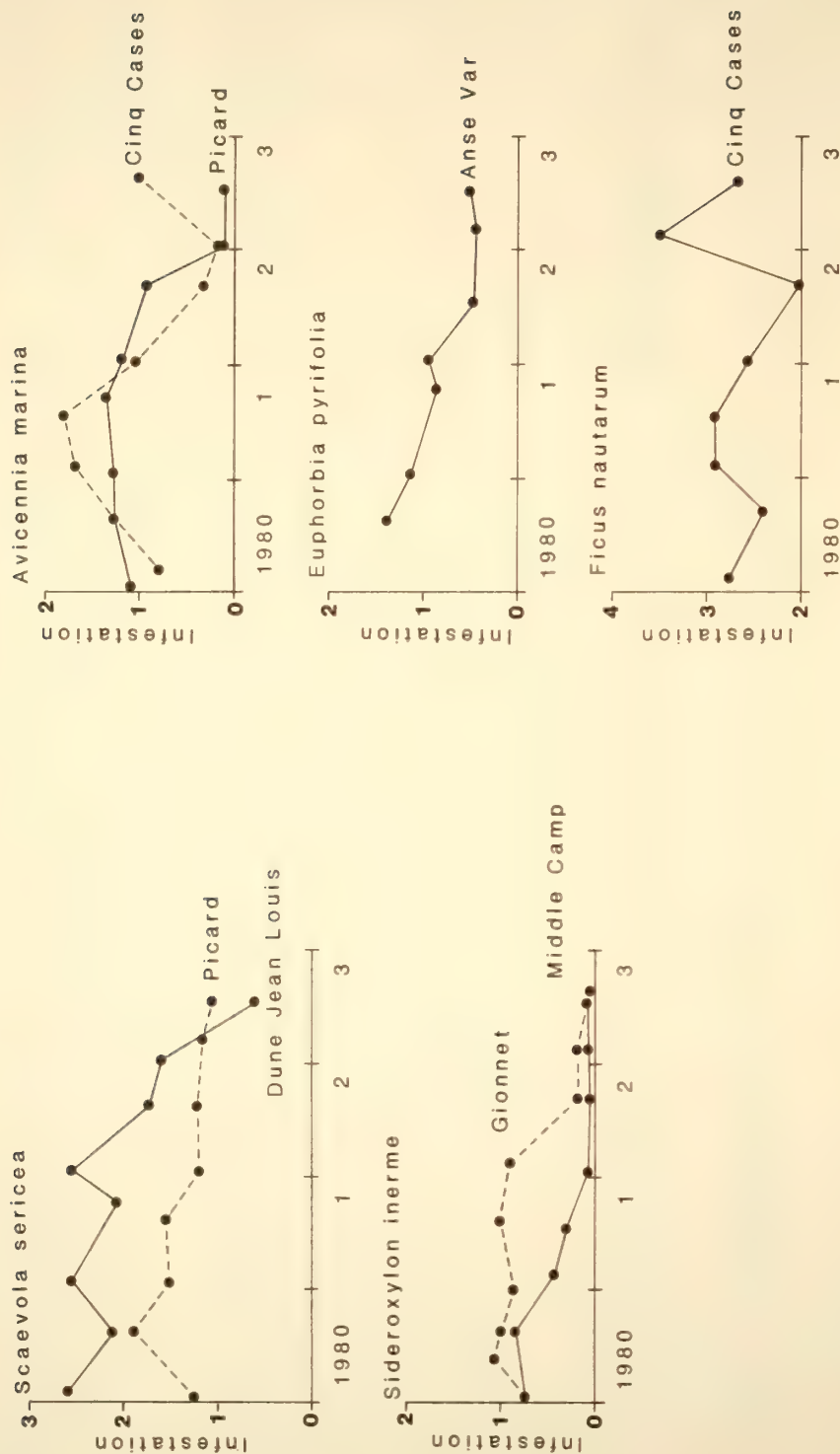


Fig. 2. The change in median coccid infestation on five susceptible species at eight locations on Aldabra Atoll monitored biannually, 1980-1983.

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EDITORS' NOTE

In line with our policy of not issuing short articles as separate numbers with their own title pages, the following articles are offered as parts of a single number.

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NON-SELECTIVE FISHING METHODS OF FUTUNA
(HORN ARCHIPELAGO, WEST POLYNESIA)

by René Galzin (1)

ABSTRACT

Futuna, a high volcanic Pacific island without a lagoon, is surrounded by an "apron reef" which emerges at low tide. During spring tides, this reef flat is subject to heavy exploitation from the island's people and domestic animals (i.e. pigs) through fishing, collecting shells, crustaceans, and echinoderms, and turning over stones and corals.

We describe two non-selective fishing methods used by the island's women: application of futu (a toxic substance obtained from the seed of Barringtonia asiatica), and construction of small rock piles to attract juvenile fish and to be dismantled after a day or two to collect the fish hiding inside.

At three stations on the sites where these fishing methods are employed, we collected, through poisoning experiments, approximately 40 species of fishes belonging to 20 families. For each species we give the number, average length and weight of the catch. In the species taken, the length ranges from 1.5 to 17.2 cm and the weight varies from 0.1 to 90.4 g.

We feel that these two non-selective fishing methods may endanger the balance of the ichthyological fauna of this island, as almost 58% of collected species were juveniles, e.g. Sargocentron rubrum, Epinephelus merra, Lutjanus monostigmus, Halichoeres margaritaceus, Acanthurus triostegus, Ctenochaetus striatus, Naso unicornis.

INTRODUCTION

A study of the coral reefs and their potential resources was undertaken on Futuna (Horn Archipelago, 2000 km north-east of New Caledonia) in November 1980.

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Futuna is a high volcanic island, 18 km long and 6 km wide, situated at 14°15' latitude south and 178°10' longitude west. There is no lagoon, but the ocean shore includes a fringing apron-reef in places almost exclusively made up of eroded calcareous pavement reef-rock. This reef flat, of narrow and variable width (maximum width 500 m), is almost totally emerged at low spring tide, and is covered by less than 80 cm of water at high tide. The geomorphology, biology and socio-economy of the Futuna marine ecosystems have been discussed elsewhere by RICHARD et al. (1982). The geomorphological observations made on the fringing reefs at Poi and Toloke (Figure 1) are as follows. The inner Poi reef is a reef-rock pavement partly covered by sedimentary accumulations. Next on the seaward side is a reef flat with widely spaced transverse ridges and furrows and, further seaward, a slightly raised pitted area. Toward the ocean, there is an inner biogenic ridge with a fragmentary covering of Melobesia and beyond that, the spur and groove area. The Toloke reef comprises a reticulated reef flat with furrows edged with crown-shaped corals. There are megablocks in the innermost area, and, seaward, a raised central zone with several branching Madreporia and Melobesia, sloping at its outer edge to the furrowed area.

The Futuna population (about 3,000 inhabitants) does not seem to live in close association with the sea. According to FUSIMALOHI and GRANDPERRIN (1980), this situation arose from cultural and religious prohibitions and taboos regarding the marine environment and dates back more than a century. GAILLOT (1961) thinks that the decline of fishing both on the reef and along the coast of Futuna today results from the regular importation of canned fish and meat. The local Economic Service (Services Territoriaux de l'Economie Rurale) believes that the appeal of the sea disappeared amongst Futunans due to 1/ the spread of a colonial-style prejudice toward the canoes previously used on the open sea; 2/ difficulties in the construction and maintenance of the very heavy, traditional canoes; and 3/ religious and tribal interdicts. For the year 1979, the Economic Service estimates the catch of fish at 32 metric tons (30 tons of ocean fish and 2 tons of reef fish).

In this paper we describe the fishing methods used by the Futunans, emphasizing in particular two traditional methods which appear to endanger fish populations. These latter are stupefying fish with futu and trapping them in piles of stones. This is not the first time that these two methods have been described in literature on fishing in the Pacific islands. We can quote among others the works of STOKES (1921), BURROWS (1936), LEONARD (1938), KRUMHOLZ (1958), LEGAND (1950), GAILLAND (1961), RANDALL (1963), BAGNIS et al. (1973), GALZIN (1977), SALVAT et al. (1978). The biometric analyses of the fish caught on the reef were made from samples obtained by poisoning.

FISHING METHODS USED ON FUTUNA

Fishing on Futuna seems to have developed in three main stages. Originally, before the arrival of European explorers (the island was discovered in 1616 by the Dutchmen LEMAIRE and SCHOUTEN) and until the end of the 19th century, the Futunans, like other Pacific Maohi peoples, were probably expert in the use of reef and ocean resources. However, as pointed out by DOUMENGE (1966), one must be wary of attributing too readily to these Polynesians a natural vocation for the exploitation of the sea. The second stage spans the period from the end of the 19th to well past half of the 20th century. During this period, Futunans became almost exclusively farmers, this mainly due to the strong influence of catholicism (Fusinalohi and Grandperrin, 1980). Finally, since 1970, the Economic Service has been trying a program of subsidies and boat construction to "reteach the sea" to the Futunans.

Methods presently used on Futuna

All methods, apart from troll line fishing, are used from the reef or on its immediate outer slope.

Troll line fishing is mainly practised around the north cape of Futuna and the south cape of nearby Alofi island. Barracuda comprise more than 70% of the catch. Jacks, frigate mackerel, tuna, swordfish and dolphins are also fished.

Dropline fishing on the outer slope has always been practised by Futunans from their small kumete (small Futunan canoes adapted originally from food bowls and without an outrigger). New deep-sea fishing techniques for catching snappers (vivanos) are currently being developed by the South Pacific Commission and ORSTOM (FOURMANOIR, 1980) with a view to teaching the local fishermen. At present, there are six boats equipped for such fishing in Futuna.

Gill nets have always been used. They are now manufactured from synthetic material (nylon) and imported from Noumea. Collective fishing with long surrounding nets seems to have been more or less abandoned and replaced by permanently-anchored gill nets. For example, at Sigave Bay (Figure 1), the number of gill nets has increased in two years from about 10 to more than 50. Nets with a 3 cm mesh can stay anchored for three to four months with catches comprising mainly kingfish Selar crumenophthalmus (locally known as atule), jacks and mullet.

Line fishing takes place by day and night on the reef slopes. This method is practised by both men and women, with the catch consisting mainly of jacks, squirrelfishes, and snappers.

The first underwater harpoon was imported from Noumea in 1961. There are now nearly 100 in use by both men and women with the catch including mainly parrotfishes, jacks, surgeonfishes, rabbitfishes and

the snapper Macolor niger.

Fishing by torchlight is practised by women on the reef at low tide on nights without moonlight. Crustacea and shellfish are also caught by this method.

Fishing with barbed spears is done by the men either on foot from the reef or by diving, but this is now dying out.

Fishing with futu and fishing with piles of stones are two methods used by the women, and will be described in detail below.

Fishing for flying fish and fishing with the use of snares are two methods described by GREZEL (1878), but they seem no longer to be practised.

Fishing with explosives: we were unable to ascertain whether this method, frequently used on Wallis, and one of the reasons for the scarcity of fish in the lagoon of this neighboring island, is also practiced on Futuna.

Fishing with futu

This type of fishing observed at Poi, tends to prevent fish from escaping by stupefying them with a vegetable poison. Two or three times a week, at low tide, an area of the inner reef flat, covered by only a few centimeters of water, is surrounded with branches and dry leaves of coconut trees. A few days in advance, about 20 Barringtonia asiatica fruits are collected and their big, round seeds grated. The powder obtained by grating the Barringtonia seeds is put in a basket which is then submerged and shaken within the enclosed area. About half an hour later, the fish begin to flounder and break surface - they are then collected with a kind of skimming net called kukutsi.

Trapping with piles of stones

This method was observed at Toloke in an area of reticulated reef with residual pools and puddles. These depressions (3 m wide by 150 m long and 0.40 m deep) have a sandy bottom over the reef pavement. The women of the village build an artificial shelter from a pile of stones, about 1 sq. m in size in one part of a basin, and this is left for a few days without being touched. On fishing day, a basket woven from coconut leaves is placed between the pile and the edge of the basin, and then the stones are removed one by one from the side away from the basket. Two or three of them are put in the basket to constitute another precarious refuge and the rest are put in the other part of the depression. The fish, which had found shelter within the pile, gradually see their refuge getting progressively smaller. All or nearly all of them seek their last shelter under the two or three stones in the basket. These stones are then removed and the fishing

process is complete.

The two methods just described above have two characteristics in common; the catch is poor for the amount of work involved, and only small specimens can be caught (the maximum size of those taken during our observation was 17 cm). A list of all species thus collected is given in Table 1.

POISONING WITH ROTENONE POWDER

Not wishing to deprive the Futuna women of their catch, yet wanting to check the biometrical parameters of the fishes thus caught, we collected fishes with rotenone (GALZIN, 1979) in the same areas several days later. The results of these catches are summarized in Table 2. At Poi, near the beach, 102 fishes were caught, with a total weight of 153 g, i.e. 1.5 g per individual. The largest fish caught was less than 10 cm long. On the same reef, but along the biogenic ridge, we caught 94 fishes with a total weight of 237 g (average weight 2.52 g). Here again, the biggest fish (Halichoeres margaritaceus) was very small (10 cm long and weighing 19.5 g). At Toloke, the fishes caught were somewhat bigger. In a depression of 13 sq. m we caught 139 fishes with a total weight of 1031.8 g - an average weight of 7.2 g each. The largest was a serranid - Epinephelus merra, weighing 90.4 g and 17.2 cm long.

These figures give an idea of the size of fish caught at low tide by the women of Futuna who gather all they can find on the reef. Among the fishes caught (Table 1) at least 26 species (58%) were at a juvenile stage: included were, e.g. Sargocentron rubrum, Epinephelus melanostigma, E. merra, Lutjanus monostigmus, Halichoeres margaritaceus, Acanthurus triostegus, Ctenochoetus striatus and Naso unicornis.

CONCLUSIONS

At low tides, the reef flat is a "rendez-vous" for both the human and animal populations of the island. The inhabitants collect all that is edible, while pigs rummage and turn over every stone, causing the destruction of sciaphile flora and fauna. However, in the absence of quantitative information on harvest rates, it is not possible to confirm the occurrence of over-harvesting.

With the two traditional fishing methods described above (futu and stones), the fish caught are almost exclusively of very small size (as noted by BURROWS, 1936). These methods thus tend not only to cause the disappearance of sedentary fish populations of the reef flat, but also to contribute to reduce fish stocks living on the outer slope: juveniles of most of the fish species living as adults on the outer slopes have to find shelter in the calmer and more trophic environment of the apron-reef where they are harvested

indiscriminately. More information is needed on the behavior of all fish species as the tides go down.

Considering the current Futunan population size, with the survival of ancient techniques of fishing as well as the introduction of new fishing methods, we observe a considerable non-selective exploitation of the apron-reef fishes on Futuna. An information campaign concerning the problems of maintaining natural stocks of fish should be launched to complete the excellent initiative already undertaken to promote and develop offshore fishing.

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REFERENCES

- BAGNIS, R., BOULIGUEUX, G., DROLLET, J. & PETARD, P., 1973 - Poisons végétaux de pêche des anciens polynésiens. SPC., Medicinal Plants, W.P., 29 : 16 p
- BURROWS, E.G., 1936 - Ethnology of Futuna. Bernice P. Bishop Museum Bulletin, 145 : 176 p.
- DOUMENGE, F., 1966 - L'homme dans le Pacifique sud. Publication de la Société des Océanistes, 19 : 633 p.
- FUSIMALOHI, T. & GRANDPERRIN, R., 1980 - Rapport sur le projet de développement de la pêche profonde à Wallis et Futuna. South Pacific Commission, 861 : 25 p.
- FOURMANOIR, P., 1980 - Mission à Wallis et à Futuna pour la pêche profonde des vivanos rouges (Etelis) à la palangre. Rapport ORSTOM : 7 p.
- GAILLOT, M., 1961 - Un type de pêche dans le Pacifique: la pêche à Futuna. Les cahiers d'Outre-Mer, 55 : 317-322.
- GALZIN, R., 1977 - Richesse et productivité des écosystèmes lagunaires et récifaux. Application à l'étude dynamique d'une population de *Pomacentrus nigricans* du lagon de Moorea (Polynésie française). Thèse de spécialité, U.S.T.L. Montpellier, 109 p. 27 fig., 30 tabl..

- GALZIN, R., 1979 - La faune ichtyologique d'un récif corallien de Moorea. Polynésie française: Echantillonnage et premiers résultats. Terre Vie, Rev. Ecol., Vol.33 : 623-643
- GREZEL, R. Père, 1878 - Dictionnaire Futunien-Français. Paris.
- KRUMHOLZ, L.A., 1948 - The use of rotenone in fisheries research. Jour. Wildlife Mangmt., 12: 305-317
- LEGAND, M., 1950 - Contribution à l'étude des méthodes de pêche dans les territoires français du Pacifique Sud. Jour. Soc. Océanistes, 6 (6) : 141-184
- LEONARD, J.W., 1938 - Notes on the use of derris as a fish poison. Trans. of the American Fish. Society, 68 : 269-279
- RANDALL, J.E., 1963 - Methods of collecting small fishes. Underwater Naturalist, 1 (2) : 6-11
- RICHARD, G., GALZIN, R., SALVAT B., BAGNIS R., BENNETT J., DENIZOT, M., & RICARD, M., 1982 - Geomorphology, ecology and socio-economy of the Futuna marine ecosystem (Horn Archipelago, Polynesia). IV Intern. Coral Reef Symp., Manila, 1 : 269-274
- SALVAT B., RICARD, M., RICHARD, G., GALZIN, R., & TOFFART, J.L., 1978 - A summary review of the ecology and reef-lagoon economy of Lau. UNESCO/UNFPA Fiji Island Reports, 4 (Canberra, ANU for UNESCO): 129-145
- STOKES, J.F.G., 1921 - Fish poisoning in the Hawaiian Islands. Occ. Paper Bishop Museum, 7 : 219-233

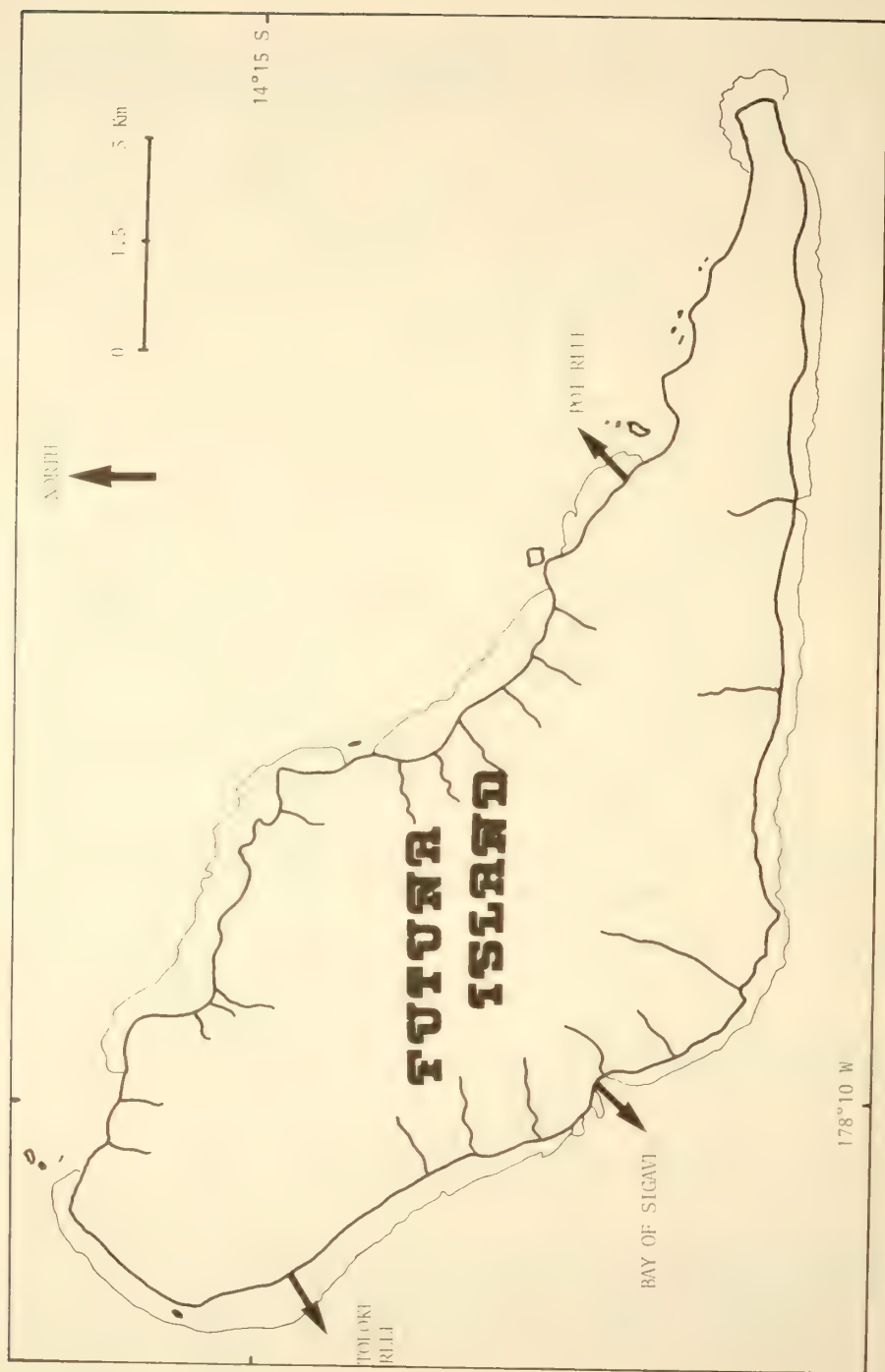


Fig. 1. Map of FUTUNA and location of the fishing sites cited in text: Poi reef - fishing with futu; Toloke reef - fishing with stone piles; and Bay of Sigave - fishing atule with nets.

		RO TENONE EXPERIMENT			Fishing with futu	Fishing with rock piles
		POI near the ridge	POI near the beach	TOLOKE		
MURAENIDAE	Echidna nebulosa (Ahl,1789)					+
	Lycodontis sp.			+		
CONGRIDAE	Conger cinereus Rüppell,1828	+				
HOLOCENTRIDAE	Sargocentron rubrum (Forskall,1775)				+	+
	" sp.			+		
SYNGNATHIDAE	Choeroichthys sculptus (Günther,1870)	+				
SCORPAENIDAE	Sebastapistes corallicola Jenkins,1902			+		
	Scorpaenodes guamensis (Quoy et Gaimard,1824)	+	+			+
SERRANIDAE	Epinephelus melanostigma Schultz,1953		+		+	
	" merra (Bloch,1793)			+		+
GRAMMISTIDAE	Grammistes sexlineatus (Thünberg,1792)	+	+	+		
PLESIOPIDAE	Plesiops caeruleolineatus (Rüppell,1835)			+		+
APOGONIDAE	Apogon aureus Lacépède,1803					+
	" cyanosoma (Bleeker,1853)	+		+		+
	" nubilus (Carman,1903)			+		+
LUTJANIDAE	Lutjanus monostigmus (Cuvier,1828)				+	
MULLIDAE	Parupeneus atrocinctus (Kner,1870)			+		
CHAETODONTIDAE	Chaetodon citrinellus Cuvier,1831			+		
	" lunula (Lacépède,1802)	+	+		+	
	Pomacanthus imperator (Bloch,1787)	+				
POMACENTRIDAE	Abudefduf sordidus (Forskall,1775)		+			
	Stegastes nigricans (Lacépède,1803)			+		+
	Chrysiptera cyanea (Quoy et Gaimard,1825)			+		
	" glauca (Cuvier,1830)	+	+	+	+	
	" leucopoma (Lesson,1830)	+		+		
	Pomacentridae sp.1 (juv.)		+			
	" sp.2 (juv.)			+		
LABRIDAE	Halichoeres hortulanus (Lacépède,1802)			+		
	" margaritaceus (Valenciennes,1839)	+		+	+	
	" marginatus (Rüppell,1835)			+		
	Stethojulis trilineata (Bloch et Schneider,1801)			+	+	
	" sp.	+				
	Thalassoma hardwickei (Bennett,1830)			+		
	" umbrotygma (Rüppell,1835)	+		+		
BLENNIIDAE	Cirripectes variolosus (Valenciennes,1836)			+		
	Istiblennius cyanostigma (Bleeker,1849)				+	
	" edentulus (Schneider,1801)		+		+	
	" periphthalmus (Valenciennes,1836)	+		+		
TRIPTYERYGIIDAE	Tripterygiidae sp.(juv.)	+				
GOBIIDAE	Bathigobius fuscus Rüppell,1828	+			+	
ACANTHURIDAE	Acanthurus nigrofusus (Forskall,1775)				+	
	" lineatus Linné,1758			+		
	" triostegus (Linné,1758)	+	+	+	+	+
	Ctenochaetus striatus (Quoy et Gaimard,1824)					+
	Naso unicornis (Forskall,1775)					+
Number of species		16	9	25	12	12

Table 1. List of fishes collected on the reefs of FUTUNA island.

		Number of species	WEIGHT in g			SIZE in cm		
			average weight	minimum weight	maximum weight	average size	minimum size	maximum size
POI	Conger cinereus	2	0.8	0.6	1.0	8.3	7.0	9.7
	Choeroichthys sculptus	1	0.2			4.1		
	Scorpaenodes guamensis	1	0.6			3.0		
	Grammistes sexlineatus	2	0.4	0.2	0.7	2.7	2.1	3.2
NEAR	Apogon cyanosoma	3	2.5	1.6	3.3	5.5	4.8	6.1
	Chaetodon lunula	2	3.9	0.6	7.3	4.2	2.4	6.0
	Pomacanthus imperator	1	1.3			3.2		
THE	Chrysiptera glauca	25	3.8	0.2	12.1	5.2	2.1	8.2
	" leucopoma	2	0.7	0.5	0.9	3.1	2.7	3.5
	Halichoeres margaritaceus	6	6.3	0.4	19.5	6.4	3.0	10.0
RIDGE	Stethojulis sp.	1	0.7			3.5		
	Thalassoma umbrostygma	3	0.2	0.1	0.3	2.4	2.0	3.0
	Istiblennius periophthalmus	4	0.8	0.5	1.2	4.1	3.5	4.7
	Tripterygiidae sp.	2	0.1	0.1	0.1	1.9	1.6	2.1
	Bathygobius fuscus	20	1.7	0.1	6.9	4.9	2.3	8.6
	Acanthurus triostegus	19	2.3	0.6	5.0	4.3	2.8	5.7
POI	Scorpaenodes guamensis	2	2.4	2.1	2.7	5.1	4.8	5.3
	Epinephelus melanostigma	5	2.7	1.2	6.3	5.5	4.3	7.8
	Grammistes sexlineatus	4	4.9	0.3	17.5	4.6	2.2	9.3
	Chaetodon lunula	1	0.2			1.9		
NEAR	Abudefduf sordidus	2	0.6	0.5	0.7	2.8	2.7	2.9
	Chrysiptera glauca	40	1.5	0.1	11.3	3.7	1.9	8.1
THE	Pomacentridae sp.	1	0.1			1.9		
	Istiblennius edentulus	1	2.0			5.8		
	Acanthurus triostegus	45	1.1	0.5	6.5	3.2	2.6	6.7
TOLOKE	Lycodontis sp.	4	6.9	1.2	16.5	13.5	8.4	17.2
	Sargocentron sp.	3	3.5	2.7	5.0	5.7	5.1	6.6
	Sebastapistes corallicola	1	5.8			6.0		
	Epinephellus merra	4	66.0	34.6	90.4	15.6	12.8	17.2
	Grammistes sexlineatus	1	0.3			2.6		
	Plesiops caeruleolineatus	1	1.6			4.8		
	Apogon cyanosoma	9	14.3	3.1	11.8	7.7	5.6	9.0
	" nubilus	1	7.7			6.6		
	Parupeneus atrocingulatus	1	3.5			6.7		
	Chaetodon citrinellus	4	9.1	4.4	13.6	7.0	5.7	8.0
	Stegastes nigricans	38	4.7	0.2	18.5	5.5	2.0	8.7
	Chrysiptera cyanea	3	0.1	0.1	0.2	2.1	2.0	2.5
	" glauca	3	3.8	2.3	6.8	5.6	4.8	7.1
	" leucopoma	1	0.1			2.0		
	Pomacentridae sp.	1	0.1			1.9		
	Halichoeres hortulanus	1	5.1			7.3		
	" margaritaceus	3	1.8	0.5	2.6	4.9	3.2	6.2
	" marginatus	6	1.2	0.1	4.1	3.5	1.7	6.4
	Stethojulis trilineata	7	5.3	1.0	12.4	6.8	4.2	9.2
	Thalassoma hardwickei	3	8.2	6.6	9.1	8.2	7.5	8.7
	" umbrostygma	8	16.8	4.7	25.8	10.3	6.8	12.0
	Cirripectes variolosus	1	0.2			2.4		
	Istiblennius periophthalmus	12	6.5	0.7	12.8	8.5	4.0	12.5
	Acanthurus lineatus	3	21.2	15.0	27.0	10.2	9.8	10.5
	" triostegus	20	2.9	0.7	8.1	4.7	3.2	7.0

Table 2. Rotenone experiments in 3 areas of the FUTUNA reef. For each station we give the number of fishes caught, the average weight and size of fishes, and the minimum and maximum weight and size of fishes.

CROISSANCE ET PRODUCTION DE CHAMA IOSTOMA DANS LE LAGON DE TAKAPOTO, TUAMOTU, POLYNESIE FRANCAISE

by Georges Richard

ABSTRACT

Chama iostoma Conrad is a species characteristic of many mollusc communities in lagoons of high islands and especially of closed atolls, in French Polynesia.

Tagging of 40 *Chama* at 4 sites led to an estimate of the growth of this species, and calculations from counts along 8 transects gave for the *Chama* population of the entire Takapoto lagoon a total of about 11 million individuals (between 1 and 2 individuals/square meter in colonized areas). Analyses of population structure and a study of total weight show that the estimated 11 million individuals represent a standing crop of 2,000 metric tons of total fresh weight including about 80 t of soft parts (corresponding to a mean soft biomass of 60 kg/hectare/year for densely populated areas, or 7.8 kg/ha/year for the whole lagoon bottom). The results of measurements made during two 8 months periods 6 months apart give a basis for calculation of a theoretical potential production of 16 tons of soft biomass per year for the entire lagoon, or 12.5 kg/ha/year for the densely colonized areas.

Chama iostoma is characterized by very slow growth rate, large standing crop, rather low productivity, and low P/B ratio. It belongs to a group of species of mediocre productivity, such as *Tridacna maxima* and *Arca ventricosa*, already studied in French Polynesia.

INTRODUCTION

Dans les études de croissance et de production, les espèces tropicales suscitent, depuis quelques années, un intérêt qui va grandissant (RICHARD, 1982). C'est le cas en Polynésie française, où de nombreux travaux (RICHARD, 1977, 1978, 1981, 1982a et b, 1983a et b, RICHARD et SALVAT, 1982) analysent la distribution quantitative, la croissance et la production ou la productivité (potentiel de production) des espèces les plus représentatives de chaque grand type de formation récifale ou lagunaire.

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Le présent travail concerne le Bivalve Chamidae *Chama iostoma* Conrad, 1837, dans le lagon de l'atoll fermé de Takapoto, une des îles du Roi Georges, archipel des Tuamotu, Polynésie française.

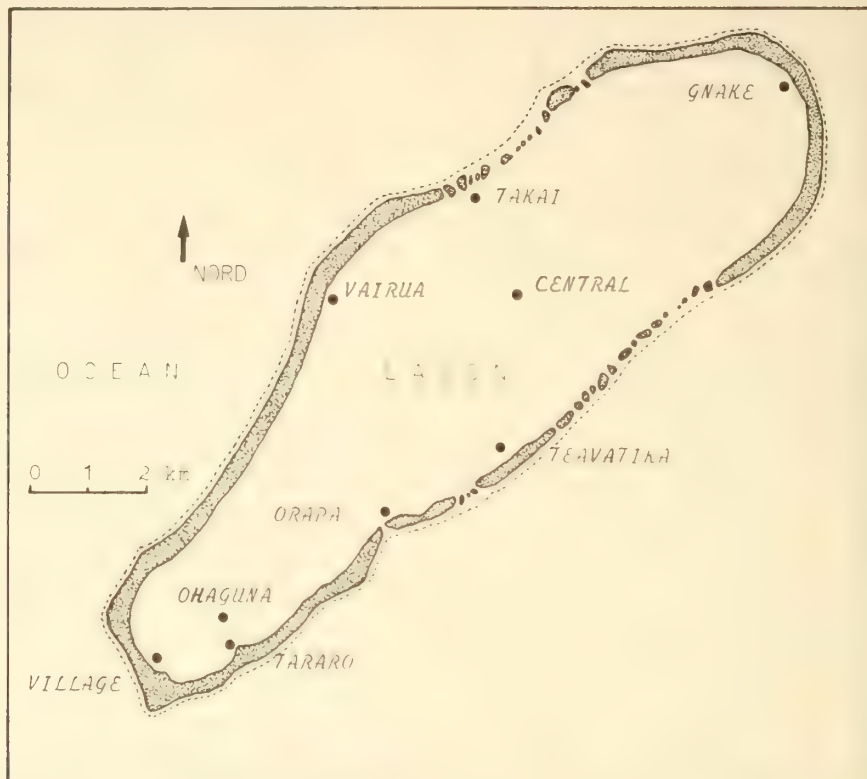


FIGURE 1: Carte de l'atoll de TAKAPOTO, montrant la position des prospections réalisées sur *Chama iostoma*, le long de la bordure lagunaire et sur les pâtés centraux.

Les Chamidae, qui appartiennent à l'ordre des Hippuritoida, ont la particularité d'être fixés au substrat par cimentation de l'une de leurs valves. Ce sont des coquilles épaisses, très encroûtées, inéquivalves, solidement fixées, ce qui pose un délicat problème dans l'estimation de la taille et du poids. En Polynésie française, la famille des Chamidae est représentée par 4 espèces:

<i>Chama brassica</i> Reeve, 1846	(Société, Marquises)
<i>Chama pacifica</i> Broderip, 1834	(Société, Tuamotu, Gambier)
<i>Chama asperella</i> Lamarck, 1819	(Société, Tuamotu, Gambier)
<i>Chama iostoma</i> Conrad, 1837	(tous les archipels)

D'avantage par sa constance que par sa réelle abondance, *Chama iostoma* est un élément caractéristique des peuplements malacologiques des lagons d'îles hautes et, surtout, des lagons d'atolls fermés.

On la distingue aisément des autres espèces de *Chama*, par les taches violettes qui colorent l'intérieur de ses valves. Nous analyserons successivement la croissance de cette espèce, puis son bilan quantitatif à l'échelle de tout le lagon de Takapoto (nombre d'individus et biomasse) et enfin sa production. Nous ferons suivre notre étude d'une brève comparaison avec les travaux précédemment réalisés sur d'autres espèces polynésiennes.

CROISSANCE

A quatre stations, situées sur la bordure lagunaire (VAIRUA, TAKAI) ou sur les pâtés centraux (TARARO, OHAGUNA) du lagon de l'atoll fermé de Takapoto (figure 1), une quarantaine de *Chama iostoma* ont été mesurés in situ (diamètre de la valve libre), entre avril et décembre 1977, d'une part, et entre juin 1978 et février 1979, d'autre part (soit deux intervalles de 8 mois). Durant ces intervalles de temps, on relève des accroissements en taille variant de 1 à 6 mm, pour des *Chama iostoma* mesurant entre 50 et 53 mm au départ de l'expérience. L'ensemble des résultats relatifs aux deux intervalles de temps nous permet de donner une expression de la croissance des *Chama iostoma* (figure 2) qui obéit aux paramètres suivants (équation de von BERTALANFFY, 1938):

$$L = 86,9 (1 - e^{-0,11t})$$

où L = taille de la coquille au temps t .

$86,9 = L_{\infty}$ = taille maximum de la coquille, atteinte quand le taux de croissance est nul.

t = âge de l'animal. (En fait, $t = t_x - t_0$, t_0 étant le temps auquel l'animal aurait eu une coquille de taille nulle; cette précision n'a pas de sens dans la présente étude et c'est pourquoi nous n'en tenons pas compte).

C'est ainsi qu'un *Chama iostoma* dont le diamètre de la valve libre mesure 13 mm a approximativement 1 an. Ceci traduit une vitesse de croissance très lente (27,8% de L_{∞} en 2 ans), mais toutefois moins lente que celle des *Arca ventricosa* (17%) dans le même lagon.

Il nous a semblé irréaliste de nous référer à la plus grande dimension de la coquille (valve inférieure fixée), pour les mesures in situ, et les données qui précèdent concernent le diamètre de la valve libre. Toutefois, il existe une relation linéaire entre le diamètre de la valve libre (X) et la taille réelle (Y) des *Chama*

$$Y = 1,05 X + 10 \quad (r = 0,9)$$

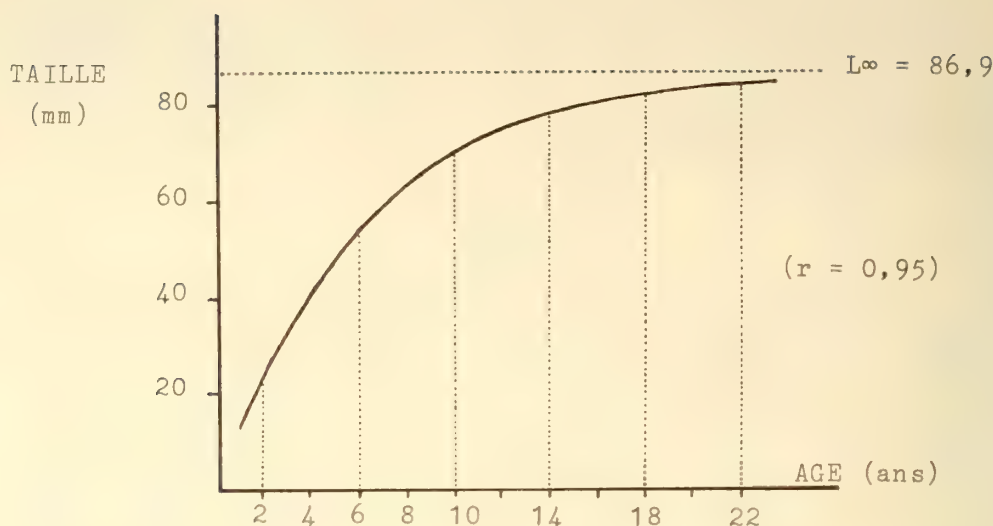


FIGURE 2: Courbe de croissance de *Chama iostoma*, calculée par la méthode de von BERTALANFFY, atoll de Takapoto.

BILAN QUANTITATIF NUMERIQUE

Le bilan quantitatif numérique de la bordure lagunaire a été dressé à partir des 4 transects de ORAPA, VILLAGE, VAIRUA et GNAKE. L'ensemble des résultats, regroupés dans le tableau A, permet d'estimer le peuplement en *Chama iostoma* de cette bordure à environ 3,8 millions d'individus.

	ORAPA	VILLAGE	VAIRUA	GNAKE	TOTAL
Longueur du "transect" (m)	90	150	112,5	137,5	520
Surface du "transect" (m ²)	150	360	225	275	1040
% de colonisation	19%	22%	33%	27%	25%
densité maximale (ind./m ²)	5,6	3,5	9	6,8	9
Nombre de <i>Chama</i> sur le "transect" (indiv.)	125	128	230	156	639
dans la zone (milliers)	975	371	1633	842	3820
Densité par m ² sur le "transect"	0,69	0,36	1,02	0,57	
dans l'aire colonisée	3,57	1,60	3,07	2,06	

TABLEAU A: Bilan des prospections quantitatives numériques réalisées sur la bordure lagunaire de Takapoto.

De la même manière, à partir des 4 transects de TARARO, TEAVATIKA, OHAGUNA et CENTRAL, dont les résultats sont regroupés dans le tableau B, le peuplement des 414 pâtés du lagon est estimé à 6,2 millions de *Chama iostoma*.

	CENTRAL	TEAVATIKA	TARARO	OHAGUNA	TOTAL
Longueur du transect (m)	102,5	67,5	75	90	335
Surface du transect (m ²)	205	135	150	180	670
% de colonisation	73%	59%	50%	44%	
densité maximale (ind/m ²)	3,6	8	2,4	8,8	8,8
Nombre d'individus					
sur le transect	155	166	91	156	568
sur le pâté (milliers)	24,94	17,59	10,715	22,042	75,29
sur la zone (milliers)	673,380	2480,19	2839,435	815,554	6208
Densité au m ²					
sur le transect	0,76	1,23	0,61	0,87	
sur l'aire colonisée	1,03	2,08	1,21	1,95	

TABLEAU B: Bilan des prospections quantitatives numériques réalisées sur les pâtés centraux du lagon de Takapoto.

Au total, en tenant compte des tests d'abondance réalisés sur le fond du lagon (densités de peuplement avoisinant 100 individus/hectare au pied des pâtés, soit un stock de 900.000 individus), on aboutit à une population totale de 10,9 millions de *Chama iostoma* pour l'ensemble du lagon de Takapoto.

BIOMASSE

Une étude des poids totaux, des poids de coquilles et de la biomasse, sur 3 populations types de *Chama iostoma*, fait apparaître que le rapport de la biomasse au poids total est de 0,04, d'une part, et que le rapport du poids de la coquille au poids total est de 0,83, d'autre part. Le complément de poids (0,13%) correspond à l'eau intervalvaire. Le tableau C donne, à titre d'exemple, les mesures concernant la station GNAKE (avril 1977).

Sur un échantillon de 100 *Chama iostoma*, la taille (diamètre de la valve libre) est une fonction linéaire du logarithme de la biomasse, selon l'équation de régression suivante:

$$Y = 35,96 X + 32,61$$

L'ensemble des données (bilan quantitatif, démographie, biomasses) permet d'estimer que les 10,9 millions de *Chama iostoma* représentent 1964 tonnes en poids frais total, dont 1630 tonnes de coquilles et 80 tonnes de biomasse. Cette dernière valeur correspond à une biomasse moyenne de 60 kg/ha pour la bordure lagunaire et

les pâtés, ou seulement 7,8 kg/ha si l'on se réfère à toute la surface des fonds lagunaires.

Dans l'ensemble du présent travail, comme ce fut le cas dans les publications précédentes relatives à la Polynésie française, traitant de l'un ou l'autre des aspects de la production en matière vivante, nous entendons par biomasse le poids frais des parties molles de l'animal.

TAILLE valve libre	TAILLE longueur	POIDS TOTAL	POIDS COQUILLE	BIOMASSE
mm	mm	g	g	g
60	70	143,0	117,5	3,5
64	80	150,7	121,7	4,9
42	49	62,2	48,2	2,3
33	45	35,0	28,9	0,9
40	46	39,7	36,2	1,6
49	55	72,0	52,8	2,5
42	50	46,8	35,8	2,0
54	64	106,9	83,4	3,7
66	78	219,0	183,9	7,9
39	55	72,9	57,9	1,8
60	77	187,0	159,5	7,1
59	68	112,5	86,7	4,9
63	72	188,2	154,4	6,8
63	80	229,9	190,2	9,2
72	84	241,8	201,9	7,3
52	65	103,4	81,1	4,8
45	58	88,5	71,6	3,7
69	89	288,7	234,5	12,9
45	60	107,8	94,1	4,1
64	69	158,1	131,0	4,7

TABLEAU C: Etude des poids totaux, des poids de coquilles et des parties molles sur une population de *Chama iostoma*, station GNAKE, atoll de Takapoto, avril 1977.

PRODUCTION

Des mesures effectuées sur 200 *Chama iostoma*, situés à trois niveaux bathymétriques de deux stations de la bordure lagunaire et des pâtés centraux (surface, -7 m de profondeur, -20 m de profondeur), nous permettent d'établir la structure démographique théorique des 10,9 millions d'individus du lagon.

A partir des données de croissance (figure 2) et de biomasse, nous avons calculé l'accroissement théorique en biomasse des *Chama iostoma* pour un intervalle de temps de 8 mois, pour chaque classe de taille séparément. Au total, cet accroissement pondéral est égal à 10,8 tonnes pour 8 mois (tableau D) et, en supposant la croissance peu variable dans le temps, à 16,2 tonnes par an.

Les quelques données rassemblées sur le recrutement et la mortalité nous font considérer que la production théorique potentiel-

le de *Chama iostoma* correspond à l'accroissement pondéral des stocks de cette espèce dans le même intervalle de temps. Ceci correspond donc à une production de 12,5 kg (biomasse) par hectare et par an pour les zones fortement colonisées, ou encore à une production de 1,6 kg/ha/an si l'on prend en compte tout le lagon.

TAILLE (T)	TAILLE (T+1)	BIOMASSE (T)	BIOMASSE (T+1)	ΔB Individuel	NOMBRE DE <i>Chama</i>	ΔB TOTAL
mm	mm	g	g	g	individus	kg
15-20	24,44	0,38	0,59	0,21	54.500	11,45
20-25	28,94	0,52	0,79	0,27	54.500	14,72
25-30	33,44	0,72	1,05	0,33	0	0
30-35	37,94	0,99	1,41	0,42	436.000	183,12
35-40	42,44	1,37	1,88	0,51	272.500	138,98
40-45	46,94	1,88	2,50	0,62	872.000	540,64
45-50	51,44	2,59	3,34	0,75	654.000	490,50
50-55	55,94	3,57	4,45	0,88	1.144.500	1007,16
55-60	60,44	4,92	5,94	1,02	1.362.500	1389,75
60-65	64,94	6,78	7,93	1,15	2.398.000	2757,70
65-70	69,44	9,34	10,57	1,23	1.798.500	2212,16
70-75	73,94	12,86	14,10	1,24	1.199.000	1486,76
75-80	78,44	17,71	18,91	1,20	381.500	457,80
80-85	82,94	24,40	25,10	0,70	163.500	114,45
85-90	-	33,61	-	-	54.500	-
90-95	-	46,29	-	-	54.500	-
				TOTAL:	10.900.000	10805 kg.

TABLEAU D: Données permettant d'établir l'accroissement en biomasse des 10,9 millions de *Chama iostoma*, en huit mois, dans le lagon de Takapoto (années 1978 - 1979).

COMPARAISON AVEC D'AUTRES ESPECES

Que l'on considère le nombre d'individus ou la biomasse de n'importe lequel des milieux représentés dans l'écosystème récifal polynésien, sa richesse est toujours le fait d'un nombre très réduit d'espèces. Dans le cadre de recherches visant à établir la productivité des complexes récifaux de cette région, ce sont justement ces quelques espèces qui ont fait l'objet d'études sur la croissance et la production.

Dans le lagon de Takapoto, cadre de la présente étude, deux autres Bivalves avaient fait précédemment l'objet de recherches identiques: *Tridacna maxima* (RICHARD, 1977, 1982a - HENOCQUE, 1980) et *Arca ventricosa* (RICHARD, 1978). Ces deux espèces affichent une croissance très lente et la vitesse de croissance de *Chama iostoma*

est intermédiaire (% de L_{∞} à 2 ans = 28) entre celle de *Tridacna maxima* (41%) et celle de *Arca ventricosa* (17%). Les trois espèces ont une production plutôt faible, découlant d'une part d'une forte biomasse et d'une forte production totale, mais, d'autre part, d'une croissance très lente et d'un mauvais rapport Production/Biomasse.

Un autre Bivalve, *Cardium fragum*, a été étudié de la même manière dans le lagon de ANAA. Cette espèce présente une croissance très rapide, mettant seulement trois ans pour atteindre 95% de L_{∞} , et les 600 millions d'individus recensés dans le lagon produiraient annuellement 2200 tonnes de parties molles (RICHARD, 1982, a, b).

Pour la classe des Gastéropodes, les études de croissance et de production ont jusqu'ici porté sur quatre espèces: *Nerita plicata*, sur un récif d'îlot d'une île haute volcanique (Moorea-Société) - *Tectarius grandinatus*, sur un récif extérieur d'atoll (Hao-Tuamotu) - *Erosaria obvelata* et *Mitra mitra* dans un complexe récifal d'île haute (Moorea). Toutes ces espèces ont des vitesses de croissance supérieures à celle de *Chama lostoma*; malgré cela, leur production est toujours inférieure, phénomène qui tient tantôt à leur faible biomasse, tantôt à un rapport P/B particulièrement bas.

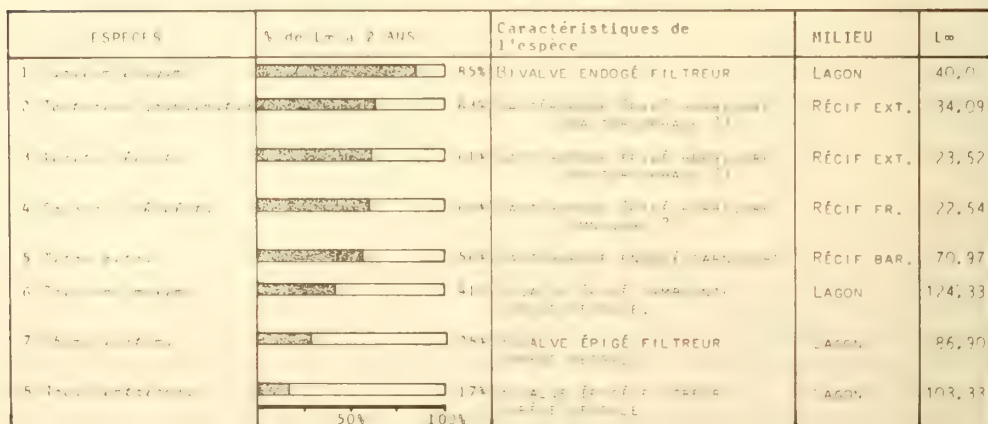


FIGURE 3: Classement des espèces étudiées, par ordre décroissant des vitesses de croissance, avec indication du milieu et du mode de vie et mention des L_{∞} .

La figure 3 donne un classement des espèces étudiées, par ordre décroissant des vitesses de croissance, avec, pour chacune d'elle, indication de son habitat et de son mode de vie; elle rappelle en outre les valeurs de L_{∞} . Quant au tableau E, il classe les mêmes espèces par ordre décroissant des valeurs de production, en envisageant successivement la production totale (en référence à l'aire du complexe récifo-lagunaire prospecté), la production par unité de surface (en référence à l'aire colonisée par l'espèce) et le rapport P/B.

PRODUCTION TOTALE (tonnes)		PRODUCTION PAR HECTARE (kg)		PRODUCTION/BIOMASSE	
1	<i>Codium fragum</i> 3500	1	<i>Codium fragum</i> 460	1	<i>Erosaria obvelata</i> 1,59
2	<i>Tridacna maxima</i> 92	2	<i>Erosaria obvelata</i> 31	2	<i>Codium fragum</i> 1,00
3	<i>Arca ventricosa</i> 49	3	<i>Tridacna maxima</i> 9,2	3	<i>Nerita plicata</i> 0,86
4	<i>Chama iostoma</i> 16	4	<i>Mitra mitra</i> 6,5	4	<i>Tectarius grandinatus</i> 0,36
5	<i>Erosaria obvelata</i> 4,6	5	<i>Arca ventricosa</i> 4,9	5	<i>Chama iostoma</i> 0,21
6	<i>Tectarius grandinatus</i> 2,2	6	<i>Chama iostoma</i> 1,6	6	<i>Mitra mitra</i> 0,19
7	<i>Mitra mitra</i> 0,9	7	<i>Tectarius grandinatus</i> 0,4	7	<i>Tridacna maxima</i> 0,18
8	<i>Nerita plicata</i> 0,05	8	<i>Nerita plicata</i> 0,01	8	<i>Arca ventricosa</i> 0,14

TABLEAU E: Classement des espèces étudiées, par ordre décroissant des valeurs de production: production totale, production par unité de surface et rapport P/B.

CONCLUSION

En ce qui concerne les paramètres de croissance, en Polynésie française, on distingue trois groupes d'espèces (RICHARD, 1982a 1983b): le Bivalve *Codium fragum* (à croissance rapide), les Gastéropodes récifaux (à croissance relativement lente), et, enfin, les

Bivalves épigés sessiles des lagons d'atolls fermés (à croissance très lente). *Chama iostoma*, objet du présent travail, est caractérisé par une vitesse de croissance très lente, intermédiaire entre celles de *Tridacna maxima* et de *Arca ventricosa*, espèces précédemment étudiées dans le même lagon (Takapoto - Tuamotu).

En ce qui concerne la production, on sépare (RICHARD, 1982a, 1983b): les espèces à très forte production (forte production totale, croissance rapide, rapport P/B élevé), les espèces à production moyenne et les espèces à faible production. Avec *Tridacna maxima* et *Arca ventricosa*, *Chama iostoma* appartient à la deuxième catégorie de Mollusques, quant à la production (forte biomasse, forte production totale, mais croissance lente et rapport P/B faible). Dans cette catégorie, *Chama iostoma* est l'espèce la moins productive, puisque les 11 millions d'individus du lagon ne produisent annuellement que 16 tonnes de chair de *Chama* (soit 1,6 kg/ha).

REFERENCES CITEES

- BERTALANFFY, von L., 1938 - A quantitative theory of organic growth. *Human Biology*, 10: 181-213.
- HENOCQUE, Y., 1980 - L'âge du bénitier, *Tridacna maxima* (Mollusque Bivalve) par examen des stries de croissance de sa coquille *Bulletin de la Société Zoologique de France*, 105, 2: 309-312.
- RICHARD, G., 1977 - Quantitative balance and production of *Tridacna maxima* in the Takapoto lagoon (French Polynesia). *Proceedings of the 3rd International Coral Reef Symposium, MIAMI*, 1: 599-605.
- RICHARD, G., 1978 - Abondance et croissance de *Arca ventricosa* dans le lagon de Takapoto (Tuamotu, Polynésie française). *Halvetes*, 9, 1: 7-10.
- RICHARD, G., 1981 - A first evaluation of the findings on the growth and production of lagoon and reef molluscs in French Polynesia. *Fourth International Coral Reef Symposium, MANILA*, 2: 637-641.
- RICHARD, G., 1982 a - Mollusques lagunaires et récifaux de Polynésie française: inventaire faunistique, bionomie, bilan quantitatif, croissance, production. *Thèse de Doctorat d'Etat, PARIS VI*, 1-2: 1-313.
- RICHARD, G., 1982 b - Bilan quantitatif et premières données de production de *Cardium fragum* (Mollusca, Bivalvia) dans le lagon de ANAA. *Malacologia*, 22, 1-2: 347-352.

- RICHARD, G., 1983 a - Growth and production of Chama iostoma in Takapoto atoll lagoon (Tuamotu - French Polynesia):abstract
International Society for Reef Studies, NIJC, abs., 24.
- RICHARD, G., 1983 b - Importance de la production malacologique dans les écosystèmes marins de Polynésie française.
Journal de la Société des Océanistes, 77, XXXIX: 77-87.
- RICHARD, G., et B. SALVAT, 1982 - Abondance et croissance de Tectarius grandinatus (Mollusca, Gastropoda) en Polynésie française.
Malacologia, 22, 1-2: 359-366.

FIRST RECORDS OF WOOD SANDPIPER, RUFF, AND
EURASIAN TREE SPARROW FROM THE MARSHALL ISLANDS

by Manfred Temme*

Ornithological observations were made incidental to other research activities from 7 to 23 November 1977 and again 21 March to 12 April 1978 on islets of Enewetak (Eniwetok) Atoll (11° 30'N, 162° 15'E) in the northern Marshall Islands. Birds also were observed during the Northern Marshall Island Radiological Survey from 11 October through 21 November 1978 when 31 islets from Likiep, Wotho, Bikini, Ujelang, Kwajalein, Enewetak, and Ailuk Atolls, as well as Jemo and Mejit Islands, were visited for relatively short periods. During these trips several new sights and breeding records for the northern Marshalls were made.

Wood Sandpiper (Tringa glareola)

I observed a Wood Sandpiper on Aomon islet, Enewetak Atoll, 9 and 21 November 1977, and saw and photographed one to three individuals 24 and 25 March and 7 and 8 April 1978 (Fig. 1). The birds were noted in the company of Sharp-tailed Sandpipers (Calidris acuminata), Golden Plovers (Pluvialis dominica), and Ruddy Turnstones (Arenaria interpres).

Aomon was the only islet at Enewetak Atoll which had permanent freshwater ponds with some marginal and low emergent vegetation. These shallow, rain-filled ponds, created in 1972 by bulldozing off most of the coral sand cover and exposing the reef substrate, were scattered over approximately six of the islet's 40 hectares.

Woodbury (1962), Pearson and Knudsen (1967), Carpenter et al. (1968), Amerson (1969), Johnson and Kienholz (1975), and Owen (1977a, b) did not mention any sightings of Tringa glareola on Enewetak Atoll or other atolls of the Marshall Islands. However, one female specimen

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(USNM 544196) in the National Museum of Natural History was collected on Runit (Yvonne) islet (Enewetak Atoll) on 8 September 1968 by the Smithsonian's Pacific Ocean Biological Survey Program (POBSP) (G. E. Watson in litt.). The specimen was collected too late to be included by Amerson (1969), and the record has remained unpublished.

The Wood Sandpiper breeds throughout northern Eurasia from Norway to the Bering Strait. It is a common migrant in Europe and southern Eurasia and winters in Africa, India, mainland southeast Asia, including the Greater Sundas and Philippine Islands, and Australia (Delacour and Mayr 1946; duPont 1971; McClure 1974; Temme 1974).

Wood Sandpipers have been recorded from Midway Atoll (Clapp and Woodward 1968), and two birds were collected at Kure Atoll (Woodward 1972). This species previously had been reported from western Micronesia. In the Marianas Baker (1971) considered it an uncommon visitor; in the Palau Islands, a regular visitor.

There can only be speculation as to the origin of the birds at Enewetak Atoll. New breeding records exist from the Pribilof Islands and the Aleutians (White et al. 1974); and numerous records (about a dozen specimens are in the USNM collection) are known from this area (G. E. Watson in litt.). That the birds could have been members of the pioneering Western Hemisphere population rather than Asian birds, which may migrate regularly as far as the Philippines and extreme western Micronesia, is suggested by the existing Alaskan and Hawaiian records. Therefore, the species should be considered a straggler and looked for elsewhere in Micronesia.

Ruff (Philomachus pugnax)

On 6 October 1978 one Ruff was observed on Kwajalein islet (Kwajalein Atoll). The bird was in its winter plumage and near Golden Plovers on the golf course. The bird was closely approached several times, and flushed to expose additional distinguishing features of this species. The relatively large size of the bird suggests that it was a male.

At Enewetak islet (Enewetak Atoll) another sighting of a Ruff was made on 21 November 1979, when O. W. Johnson pointed out a bird not familiar to him. Subsequently several photographs were obtained (Fig. 2). The bird appeared smaller than the one seen on Kwajalein islet and may have been a female (Reeve). It stayed in close company with 64 Sharp-tailed Sandpipers.

These two records, in addition to one collected on Enewetak (Clapp in litt.), are the only ones known for the northern Marshall Islands. Ruffs have been recorded from the Palau Islands (Owen 1977a), and specimens have been collected at Kure Atoll (Clapp and Woodward 1968) and Pearl and Hermes Reef in the northwestern Hawaiian Islands (Amerson, Clapp, and Wirtz 1974) and at Johnston Atoll (Amerson and Shelton 1976).

The Ruff breeds throughout northern Eurasia from Denmark to the Bering Strait and winters in Africa, Pakistan, Burma, southeast China and casually in Japan, Taiwan, Philippines, Borneo, and Australia (A.O.U. 1957; McClure 1974; Temme 1974; King and Dickinson 1975). It is a straggler in the Marshall Islands.

Eurasian Tree Sparrow (Passer montanus)

On 6, 7, 9, 29, and 31 October 1978 the only sparrow I observed on Kwajalein islet (Kwajalein Atoll) was the European Tree Sparrow. Several birds were seen in coconut palms near the town plaza and at gas tanks. Previously only the House Sparrow (Passer domesticus) had been noted (sight and call note records only) from this islet (Amerson 1969). However Clapp (in litt.) suggests that P. montanus has been newly introduced, perhaps via the Hawaii-Kwajalein-Guam Continental Airlines flight. Anderson (1981) saw a maximum of 20 Passer sp. in 1977 but did not make specific identification.

The European Tree Sparrow replaces the House Sparrow at about the 90th meridian and is common in South Asia (McClure 1974; King and Dickinson 1975). In the Philippines it is an introduced species and frequents human habitations (own obs.). It has been reported in Micronesia apparently only from the Marianas (Owen 1977b). The observation of this introduced species constitutes the first recognized sight record for the northern Marshall Islands, though they may have been there a year earlier (Anderson 1981). These birds also were observed there by Clapp (in litt.) in 1979 (summer).

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Literature cited

- American Ornithologist's Union. 1957. Checklist of North American birds, fifth ed. Amer. Ornithol. Union, Baltimore.
- Amerson, A. B., Jr. 1969. Ornithology of the Marshall and Gilbert Islands. Atoll Res. Bull. 172:1-348.
- Amerson, A. B., Jr., R. B. Clapp, and W. O. Wirtz, II. 1974. The natural history of Pearl and Hermes Reef, northwestern Hawaiian Islands. Atoll Res. Bull. 174:1-306.
- Amerson, A. B., Jr. and P. C. Shelton. 1976. The natural history of Johnston Atoll, Central Pacific Ocean. Atoll Res. Bull. 192:1-479.
- Anderson, D. A. 1981. Observations of birds at Ujelang and other northern Marshall Islands atolls. Micronesica 17:198-212.

- Baker, R. H. 1951. The avifauna of Micronesia, its origin, evolution and distribution. Univ. Kansas Mus. Nat. Hist. Publ. 3:1-359.
- Carpenter, M. L., W. B. Jackson, and M. W. Fall. 1968. Bird populations at Enewetak Atoll. Micronesica 4:259-307.
- Clapp, R. B., and P. W. Woodward. 1968. New records of birds from the Hawaiian Leeward Islands. Proc. U. S. Nat. Mus. 124 (3640):1-39.
- Delacour, J., and E. Mayr. 1946. Birds of the Philippines. MacMillan, New York.
- duPont, J. E. 1971. Philippine Birds. Delaware Mus. Nat. Hist., Greenville.
- Johnson, O. W., and R. J. Kienholz. 1975. New avifaunal records from Eniwetok. Auk 92:592-594.
- King, B. F., and E. C. Dickinson. 1975. A field guide to the birds of South-East Asia. Houghton Mifflin Comp., Boston.
- McClure, H. E. 1974. Migration and survival of the birds of Asia. Bangkok, Thailand, United States Army Medical component, SEATO.
- Owen, R. P. 1977a. New bird records for Micronesia and major island groups in Micronesia. Micronesica 13:57-63.
- Owen, R. P. 1977b. A checklist of the birds of Micronesia. Micronesica 13:65-81.
- Pearson, D. L., and J. W. Knudsen. 1967. Avifauna records from Eniwetok Atoll, Marshall Islands. Condor 69:201-203.
- Temme, M. 1974. Beitrag zur Kenntnis des Vorkommens ostpaläarktischer Limikolen auf Mindoro, Philippinen. J. Ornithol. 117:100-104.
- White, C. M., F. S. L. Williamson, and W. B. Emison, 1974. Tringa glareola - a new breeding species for North America. Auk 91:175-177.
- Woodbury, A. M. 1962. A review of the ecology of Eniwetok Atoll, Pacific Ocean. Univ. Utah, Inst. Environment. Biol. Res.:1-123.
- Woodward, P. W. 1972. The natural history of Kure Atoll, northwestern Hawaiian Islands. Atoll Res. Bull. 164:1-318.

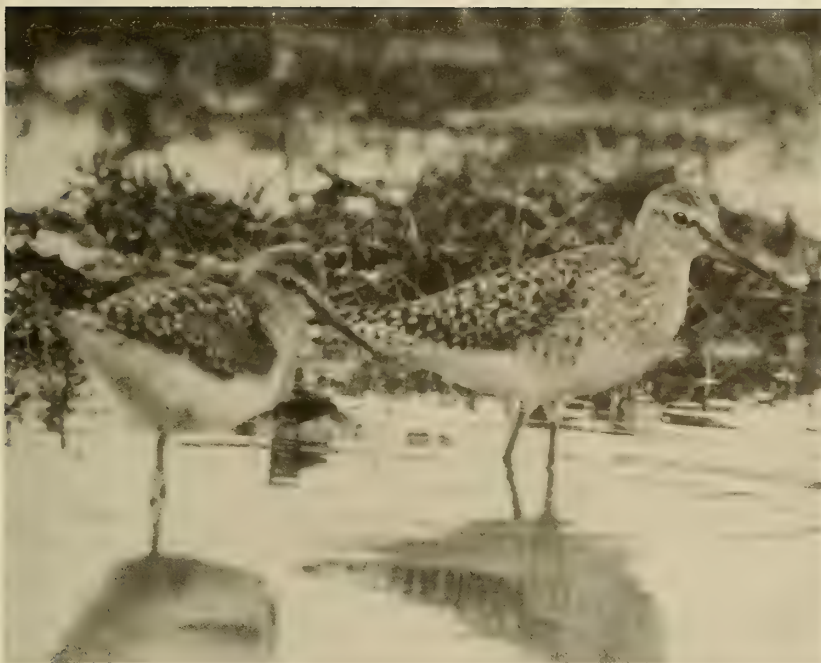


Fig. 1. Wood Sandpiper Tringa glareola on Aomon islet, Enewetak Atoll, Marshall Islands (April 8, 1978)

Fig. 2. Ruff Philomachus pugnax among Sharp-tailed Sandpipers Calidris acuminata on Enewetak islet, Enewetak Atoll (November 17, 1978)



CLASSIFICATION OF EMERGENT REEF SURFACES

by F. R. Fosberg

Anyone who has attempted serious bibliographic work on "coral reefs" (*sensu latissimo*), or on islands, or on coastal zone features, has likely had a feeling of being overwhelmed by the sheer amount of published (and unpublished) information that has accumulated. The realization inevitably leads to analytical attempts to break the mass down into more manageable fragments or "fields". These are normally arranged into classifications of one sort or another. The nature of such analyses and classifications ordinarily is determined by and reflects the particular interests and biases of those who make them.

Sometimes, in any area of knowledge, one finds that a more or less satisfactory scheme already exists, and can be accepted and used or modified. Most often, because of differences in purposes or objectives of one's investigation, available schemes are not entirely appropriate and must be modified to suit new requirements, or new schemes must be worked out. This may be true at any level in the hierarchy of the classification of knowledge.

The present attempt resulted from an essay on the present state of knowledge of the floras and vegetation of emergent reef surfaces--the terrestrial plant cover of relatively recent emergent reefs.

Rough or vague arrangements of information on these may be found in almost any consideration of the vegetation of islands, or of a single island or group, less frequently in floristic works. These schemes usually assume a knowledge or familiarity with "the obvious" and often use undefined general units or local folk terms and concepts. They are often more or less satisfactory for the immediate area concerned, but become less so or unsatisfactory when extended, generalized, or adapted to other regions. The scheme here presented evolved because none of the familiar ones was broad enough, precise enough, or exactly served to facilitate understanding of the botany of emergent reef surfaces.

Even the term "emergent reef surface" presents difficulties. Obviously it means the surface of a reef that is above high tide level. But what about fossil reefs? In a sense, all even slightly emergent reefs, even elevated beach-rock, are fossil reefs. How far back should one go geologically? Ideally, emergent reef surfaces should be surfaces that have never been buried by massive sedimentary deposits or by volcanic ejecta--either ash or lava--though they may bear accumulations of sand, gravel, boulders or other reef-derived material. They are calcareous in composition except for small amounts of pumice or other water-borne or wind-borne substances. This means that the plant cover of these surfaces derives from successful plant colonizations over the period since the emergence of the reefs, by lowering of sea-level, tectonic uplift, or accumulation of water-carried calcareous material (bars, spits, or storm ridges).

This definition of emergent reef surfaces excludes most geologically old or ancient reefs, as their exposed surfaces have mostly been formed by erosion of overlying non-reef material. Usually their limestones are of quite different character than those of the more recent reefs that have never been buried. Their floras bear little or no relation to the strand flora or enriched strand flora of modern emergent reefs. In general, fossil reefs of Quaternary to Recent age provide emergent reef surfaces. Some are classed as Plio-Pleistocene, and in rare instances as Miocene (e.g. the Barrigada Limestone of Guam, and limestones on Mangaia, Cook Islands). Of course, there has been more or less chemical erosion, and even abrasion, on all or most such surfaces.

The following scheme will provide a basis or framework for correlation of the plant species and vegetation with appropriate variations in the emergent reef habitat. It is arranged in outline form, but with sufficient descriptive comment to make the distinctions and relationships clear. The principal basis of the classification is topographic and locational, but these factors are strongly correlated with degree or lack of induration, and degree of chemical erosion and consequent roughness or ruggedness of the surface. Almost all of the units listed show differing facies in areas of greater or less rainfall. Solution of the limestone and consequent change or degradation of the surface may be more active in areas of greater rainfall, as may the effects of plant roots and humus. Different burrowing animals may affect the surfaces in different ways, and their distribution may be influenced by the climate. The rainfall factor strongly influences the vegetation and flora directly, and the more abundant soil formation in wet areas produces perceptible effects on the reef surface. Salt spray, too, affects the nature of the erosion of coral limestone, in a way not fully understood, at least by me. This will be described at an appropriate place in the classification.

- (1) A convenient primary subdivision of emergent reef surfaces is into (1.1) oceanic, that is, formed on or around islands which have never had any connection or close proximity to continental or major island land-masses, vs. (1.2) continental, formed on the shores of continental

or large island land-masses. These categories are appropriate for biological purposes, because of the differences in complexity of oceanic vs. continental biotas (see 1.2 below).

(2) Oceanic emergent reefs are either (2.1) atolls and table reefs, not closely associated with non-calcareous islands, or (2.2) fringing and barrier reefs, formed around higher, usually volcanic islands.

(3) Atolls and table reef surfaces are either essentially at (3.1) sea-level or (3.2) relatively uplifted.

(4) Essentially sea-level reefs may be of (4.1) loose, unconsolidated material, sand, gravel or boulders, or of (4.2) indurated such material or in-place reef structure; either kind may bear temporary local accumulations of loose sand (dunes) or gravel storm-ridges which may reach over 3 m, rarely considerably more.

(4.1) Unlithified reef surfaces, including sand cays, islets and bars, are loose accumulations of sand-size or larger foraminiferal tests and fragments or entire skeletons of other calcareous animals and plants. In areas where the ocean is generally only slightly or moderately turbulent there may be, especially on lagoon margins, deposits of precipitated or trituated silt-size material. This material is usually blown away by wind but may be held by algal crusts or evaporite salt crusts. Cays of loose material tend to be changed frequently by storms and wave action, at least until they become well-stabilized by vegetation or their margins become protected by intertidal beach-rock formation.

(4.2) Lithified atoll islets and table reefs have at least parts of their surface of a cemented reef-conglomerate or a lime-sandstone platform, or of bedded atoll phosphate rock (Jemo soil). There is little agreement as to the circumstances under which such lithification takes place, but the physiography frequently suggests that it happened during previously higher post-glacial sea-levels of 2 or 3.5 m above present. The phosphatic lithification is associated with present or past Pisonia grandis forests and roosting or nesting of sea-birds. Lithified surfaces on these very low islands are usually flat, but older ones may be rough or pitted by chemical erosion.

(5) Elevated reefs may be either (5.1) slightly raised (4-8 m) or (5.2) substantially more so, and almost always at least mostly indurated, but often with some perched loose material, storm- or wind-deposited. Surfaces may be either relatively flat, or dissected; older strongly elevated reefs may be eroded into (5.3) karst topography, but karsts also may be cut into much older limestones of other than reef origin. This distribution may not be easy to establish.

(5.1) Slightly elevated atolls and table reefs. Usually partly of sand or gravel, but at least with a core or an extensive platform of conglomerate or "reef-rock" that extends locally to more than 4 m elevation. The lithified surface is flat and covered by loose deposits, or bare and either a flat "pavement" (platin) or a pitted, pinnacled,

or intricately dissected or eroded into a sharp "fretwork" (champignon), or less so (pavé). These parenthetical terms are Creole, used in the Western Indian Ocean islands, especially Aldabra. A Polynesian term for dissected slightly elevated surfaces is feo. Caribbean terms for sharply dissected surfaces are "dog-tooth" and "iron-shore". The very sharply and finely dissected or "fretwork" facies of this surface seems associated in some way with proximity to salt-water, perhaps exposure to salt spray. Simply pinnacled facies may be found more inland, out of reach of heavy spray. How sea-water, which is said to be super-saturated with calcium carbonate, can cause or accentuate chemical erosion of limestone is not clear. Long-term experimental work on this problem would be desirable.

(5.2) Elevated flat-topped reefs (10-200 m or more) not closely associated with high islands or continental shores are not numerous, and the surfaces of most of them have been destroyed or completely altered by phosphate-mining. On Nauru, for example, an artificial mini-karst or deeply (to 10 m) pitted-pinnacled new surface has been produced. Natural pinnacled surfaces exist on Henderson Island, nearly undisturbed. On Henderson, also, are relatively smooth surfaces of loose material or soil. Such islands are generally surrounded by cliffs, with or without a narrow flat coastal strip or shelf at or just above sea-level at base. The cliffs may be vertical or very steep, with, in places, ledges or caves. They may be undercut, intertidally.

(5.3) True karsts are a third sort, more often near larger islands (or on continental shelves). They are very rugged, with sharp peaks and ridges, steep rough slopes, and are often deeply undercut at base. Without careful geological observation it is not always certain whether they are cut in elevated reefs or in ancient limestones of other than reef origin. Good examples are the southern islands of the Palau group (except Angaur and Peliliu) and the Lau Group of Fiji (possibly continental rather than oceanic).

(2.2) Reefs around high islands. The difference between these and those listed above is important biologically because of the enrichment of the biota due to the proximity to the more diverse biota of the high islands. As with the reefs not associated with high islands, those in this category may be divided into (6.1) essentially sea-level and (6.2) significantly elevated above sea-level.

(6.1) Sea-level-fringing and barrier reef emergent surfaces are similar in most ways to those of atoll islets. The islets on barrier reefs are, in fact, scarcely distinguishable from those of atolls except for the proximity of a high island. Emergent fringing reefs may present a smooth, abraded surface, or a variously pitted one. Non-calcareous earth may wash or blow down onto the fringing reef surface, making possible the growth of more species of plants.

(6.2) Elevated reefs surrounding high islands may be (7.1) slightly elevated or (7.2) strongly elevated, as are those in open sea.

(7.1) Slightly elevated reefs, either barrier reef islets or fringing reefs. These present a series of surface features similar to those described above for slightly elevated atolls and table reefs (see 5.1).

(7.2) Elevated reefs - peripheral and terraces on slopes. These are frequently deeply dissected, sometimes labyrinthine. The "makatea" surrounding some South Pacific islands (e.g. Austral Islands) is an example.

(1.2) Continental reefs, lining coasts of continents and continental islands, comprise a series of categories parallel to that outlined above for oceanic island reefs but, by their geographic positions, carrying richer floras and more complex vegetation. Descriptions of such categories need not be repeated here. Continental reef surfaces are numerous in the Caribbean and western Pacific regions.

The above scheme is summarized in the accompanying diagram.

In a review of this paper the suggestion was made that the classification here proposed be related to previous classifications of the same phenomena. The literature on reef-classification is enormous and I am familiar with much, but by no means all, of it. By far the greater part of it concerns submerged reef features and the processes that produce them, the preoccupation of most students of coral reefs. Emergent features are mentioned incidentally, or in relation to such features as soils, geology, geomorphology, and land ecology. Descriptions usually apply to specific examples--atolls, islands, or localities. Many of the descriptive terms, and the phenomena referred to, are of wider occurrence or application, and are useful for general descriptive purposes while others are too limited or specific to be generally applicable. Many of the terms and features used or described in the present attempt are from one or more such papers, but nowhere have I seen a comprehensive description or classification of emergent reef surface phenomena. The one that comes closest is in the sections on Terrain and on Islets, as well as scattered through the text, of my volume on Military Geography of the Northern Marshall Islands (1956). This includes and describes many of the surfaces treated in the present paper, and furnishes much of its substance. However, it is limited to the surfaces found on the sea-level atolls of the Northern Marshall Islands and is not organized into a classification. It does not provide the inclusive array of emergent reef surfaces that exist and is not thoroughly applicable to all known atolls and barrier reef islets. Elevated surfaces are not treated at all.

I have read and been impressed by Stoddart's pungent discussion of the confused state of reef terminology in *Coral Reef Research Methods* (Stoddart and Johannes, 1978). I hope I have not contributed further to the confusion he described. It is noticeable that, after this pertinent discussion, the volume does not offer a terminology which would help avoid the difficulties pointed out, nor does it include any attempt toward a classification or orientation in the kinds of reefs or reef surfaces.

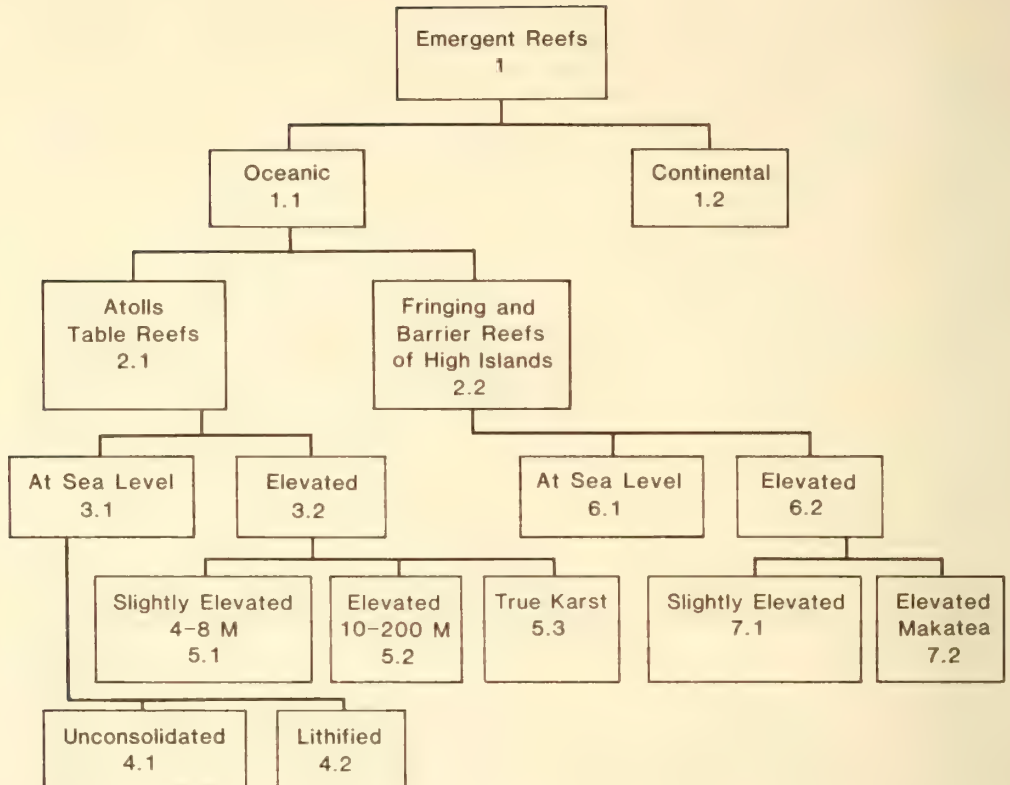


Fig. 1. Diagram of Classification of Emerged Reef Surfaces

REFERENCES CITED

- [Fosberg, F. R.]. 1956. Military Geography of the Northern Marshall Islands. 320 pp. pub. by Office of the Engineer, Hq. U.S. Army Forces Far East, [Tokyo]. (Unclassified).
- Stoddart, D. R. and R. E. Johannes, eds. 1978. Coral Reefs: Research Methods. 581 pp. UNESCO, Paris.

BOTANICAL VISITS TO KRAKATAU IN 1958 AND 1963

by F. R. Fosberg

Twice, on December 20, 1958 and December 9, 1963, while visiting Java for UNESCO Humid Tropics Program activities, I had the privilege of seeing Krakatau Island volcano. The recent celebration (1983) of the 100th anniversary of the world's greatest explosion in recorded history, and the publication of the complete collected writings about the Krakatau eruption (reviewed briefly below), brought to mind observations I made on my visits, 25 and 22 years back.

Brief notes on the conditions of Anak Krakatau (Krakatau's Baby), the new cone that appeared on the site of the center of the former large volcanic cone may be of some interest. Comparison of the list of plants seen and collected on Anak in 1963 with lists recorded before and after may contribute to understanding of the ability of plants to cross water barriers and to colonize new volcanic substrata. A valuable addition to this account is a list of the collections made, at my suggestions, on Anak Krakatau in August 1971, by Professor Mildred Mathias and her colleagues, Phung Trung Ngan and W. Soegeng Reksodihardjo. Her specimens are at U.C. Los Angeles. Mine are in the U.S. National Herbarium, Smithsonian Institution, Washington, D.C.

On December 20, 1958, aboard the Indonesian oceanographic research vessel Samudera, a turn was made around Anak Krakatau, as close in as was prudent, during a period of pulsating explosive eruptions. My attention was so held by the excitement of the eruption that I did not write much down. I merely noted several Casuarina shrubs on the south slopes. A brief, edited, account of my 1958 and 1963 notes follows.

The three remnants of the original volcano, very steep and rugged, are arranged in a broken circle, densely wooded to their summits except for vertical cliffs. Time was not available to land on them. The group reminded one of Maug, in the northern Marianas, except on a much larger scale and densely wooded.

Anak, during our circuit in 1958, was in a state of continuous pulsating activity. Explosions occurred every few minutes, throwing ash and rocks to considerable heights. From the rim of a large crater smooth slopes of dark brown ash and cinders ended in low wave-cut cliffs, except at one end where the slope reached beach level. Apparently some coral debris may have been cast up here, as the top of the beach, otherwise black, is light colored. Here a small patch of Casuarina had reached tree size. Three or four similar trees were seen scattered above on the slopes. Otherwise no vegetation was seen through binoculars.

The forest on the three outer, older islands was luxuriant to the tops, except on the cliffs. Casuarina is an important component, mostly in patches. Terminalia catappa was perhaps the most important tree in area, covering much of the lower slopes. However, there were a good many other species and the vegetation was generally a dense mixed forest. No grass was visible except on the steep inner wall.

On our visit in December 1963, again under UNESCO auspices, the volcano was quiet, though producing much steam and sulphur dioxide. We were able to land at the northeast corner, where the same clump of Casuarina, seen in 1958, was now much taller. The steam, in great white billows, was mainly coming from the low south side of the crater.

From the sea, before landing, we could examine the mountain with binoculars. The crater was about one third or half the width of the island. The south side had been undercut and slumped, exposing very clear bedding of the ash. From fairly close, a scattering of small plants, grass tufts, could be seen on the slopes above the Casuarina clump, and one fair-sized Casuarina some way up toward the crater. The lowest point on the crater rim appears to be where a lava flow has come forth and down the south slope, spreading out fan-wise at the base. The flat ground around the Casuarina clump at the northeast corner is grassy, the grass extending westward along the north shore, to a smaller sparse patch of Casuarina, mostly appearing dead.

Ashore the flat area of grassy vegetation contained about 25 species, some of them only represented by one or more germinated seeds. They are listed below. Only the abundant sterile tufts of Saccharum spontaneum and a few scattered Casuarina ascended part way up the slopes. Land-crab holes were seen on the slope as much as 300 m from the sea, and dead grasshoppers even farther up.

Huge splatter-bombs have been thrown at least 2/3 the way from the crater to the sea, smaller ones even farther. Nearer the top they practically cover the slope, along with scattered pieces of a dense porphyry, several colors of scoria, some pumice, and a few enormous fusiform bombs.

Inside the crater were white bedding, and a complex of cones and vents, brightly stained with sulphur. The congealed flow seen from the sea runs along the area of cones and spills over the rim to the south. Steam and sulphur dioxide discouraged much lingering at the top. We climbed only the north slope and descended to the northwest corner.

On the flats of cinders and volcanic sand were low thickets of Casuarina and patches of tall Saccharum spontaneum, sod of Ischaemum and mats of Ipomoea pes-caprae and Canavalia rosea, which seemed to have repeatedly been almost killed, probably by fumes. Some of the Casuarina was dead or almost so, as well as the Morinda and Calophyllum. Cassytha was mostly dead. Ischaemum leaves were dead but the stems were still green. All species seen living were collected, but there were also scattered wave-cast seeds that had not germinated. Time was too limited to gather these.

The following list includes the species recorded by J. van Borssum Waalkes in 1960 (Ann. Bogor. 4:5-64) of all species collected or observed on Anak by himself or other visitors before all the vegetation was destroyed by the 1952 eruption. Pre-1952 records are indicated by W, van Borssum Waalkes collections by W with his collection numbers; Fosberg records in 1963, with collection numbers, by FRF; and 1971 records by Mathias et al. by MEM plus collection numbers. Field notes and comments of interest are included in parentheses after the appropriate collection numbers. Adjustment of the nomenclature has been made where discrepancies between the lists are found.

Lygodium flexuosum (L.) SW.

MEM 25

Nephrolepis falcata (Cav.) C. Chr.

MEM 28

Nephrolepis hirsutula (Forst. f.) Presl

W 1068 (on slopes to 50 m)

Nephrolepis radicans (Burm. f.) Kuhn

MEM 29

Pityrogramma calomelanos (L.) Link

W 1069 (on slopes to 50 m, fair numbers seen in 1951), MEM 32

Cycas circinalis L. (*Cycas rumphii* Miq.)

W (one plant seen)

Pandanus tectorius Park.

W, FRF 44549 (only a few plants seen), MEM 30

Imperata cylindrica Beauv.

W 1081 (small area, only, on E side), FRF 44555 (rare, one tiny patch seen), MEM 21

Ischaemum muticum L.

W 1083 (fairly large number seen in 1951), FRF 44551 (very common, forming loose sod locally), MEM 24

Saccharum spontaneum L.

W 1075, FRF 44556 (commonest plant on island, mature ones on flat, smaller ones on cinder slopes), MEM 35

Spinifex littoreus (Burm. f.) Merr.

W 1070, FRF 44547 (occasional on open beach), MEM 37

Thuarea involuta (Forst. f.) R. & S.

W 1074, MEM 39

Cyperus javanicus Houtt.

W 1071, FRF 44552 (rare, one tuft seen), MEM 10

Fimbristylis cymosa R. Br.

FRF 44553 (rare, one tuft seen)

Remirea maritima Aubl.

FRF 44550 (very local in sand)

Cocos nucifera L.

W (germinating nuts seen, probably both washed ashore and planted by man), MEM 8

Nypa fruticans Wurmb.

W

Musa paradisiaca L.

W

Eulophia pulchra (Thou.) Lindl. (*Eulophis macrostachya* Lindl.)

MEM 14

Casuarina equisetifolia L.

W 1082, FRF 44562 (common, spreading up slopes; seen in 1958),
MEM 6

Piper aduncum L.

MEM 31

Ximenia americana L.

MEM 42

Ficus septica Burm. f.

MEM 18 (observed only)

Ficus fulva Reinw. ex Bl.

MEM 17

Cassytha filiformis L.

W 1075 (fairly large numbers seen in 1951), FRF 44545 (abundant),
MEM 5 (evidently common, associated with several host plants)

Hernandia sonora L.

W (very young seedlings, only)

Albizia retusa Benth.

MEM 1

Canavalia rosea (Sw.) DC.

W 1077, FRF 44544 (very common), MEM 4

Derris trifoliata Lour.

W

Desmodium umbellatum (L.) DC.

W 1078, FRF 44559 (occasional), MEM 11

Erythrina variegata L.

W (seen earlier but not in 1951), FRF 44560 (rare, one plant seen), MEM 13

Phaseolus sp.

W

Pongamia pinnata (L.) Pierre

W, FRF 44565 (occasional), MEM 33

Vigna marina (Burm.) Merr.

W, MEM 40

Murraya exotica L.

W

Xylocarpus granatum Koen.

W

Antidesma sp.

W

Euphorbia chamissonis (Kl. & Gke.) Boiss.

MEM 16

Dodonaea viscosa L.

MEM 12 (seedling)

Colubrina asiatica (L.) Brongn.

MEM 9

Cissus repens Lam.

W

Hibiscus tiliaceus L.

FRF 44564 (rare), MEM 20

Calophyllum inophyllum L.

W 1080, FRF 44566 (occasional, mostly dead), MEM 3 (seedling)

Barringtonia asiatica (L.) Kurz

W (seen earlier but not seen in 1951), FRF 44567 (rare, seedlings only), MEM 2 (seedling)

Rhizophora mucronata var. *stylosa* (Griff.) Schimper (*Rhizophora stylosa* Griff.)

W

Terminalia catappa L.

W 1083, FRF 44563 (occasional), MEM 38

Melastoma malabathricum L. (*Melastoma polyanthum* Bl.)

MEM 26

Cerbera manghas L.

W, MEM 7

Ipomoea littoralis Bl. (as *Ipomoea gracilis* R. Br.)

FRF 44557 (rare, one plant in thicket), MEM 22

Ipomoea pes-caprae ssp. *brasiliensis* (L.) v. Ooststr.

W 1076, FRF 44548 (common), MEM 23

Clerodendrum inerme (L.) Gaertn.

FRF 44561 (rare, one plant seen)

Premna obtusifolia R. Br.

FRF 44558 (occasional), MEM 34

Guettarda speciosa L.

MEM 19

Morinda citrifolia L.

W 1067, FRF 44546 (occasional), MEM 27

Scaevola sericea L.

W 1079 (common, but much eaten by grasshoppers), FRF 44568 (occasional), MEM 38

Chromolaena odorata (L.) King & Rob. (*Eupatorium odoratum* L.)

FRF 44554 (occasional), MEM 15

Wollastonia biflora (L.) DC. (*Wedelia biflora* (L.) DC.)

MEM 41

Since this paper was written an excellent article on Krakatau, by Ian W. B. Thornton (Ambio 13:216-225, 1984), has come to my attention. This article summarizes what was on record as to the recolonizations over the 100 years following the great explosion in 1883, and adds observations made during the Hull University Expedition in 1983, by J. R. Flenley and K. Richards, as well as by the author himself, on three visits.

It may seem superfluous to publish the observations made in 1958, 1963 and 1971, after the excellent Thornton account, However, the

information offered here was not available to Thornton, and partially fills in the period between two total or almost total sterilizations of Anak Krakatau by major eruptions (1952 and 1972). It is unfortunate that a collection made by Kostermans at some time between 1952 and 1963 could not have been included. According to Kostermans (personal communication in 1964) the specimens collected were incorporated into the Bogor herbarium and no list of them was preserved. Retrieval of the record of species with any degree of completeness would be impractical. It is hoped that the results of the series of investigations, 1982-1984, mentioned by Thornton, at least so far as they concern Anak Krakatau plants, may be assembled and studied with an aim to better understand the processes of dispersal, establishment, increase, decrease, and disappearance, chance and probability, in relation to succession. A more balanced comparison with the detailed studies of Surtsey (Iceland) may then be possible.

Thornton (p. 224) quotes Tagawa (1983) as listing Nephrolepis tomentosa v.A.v.R. as one of the dominant pioneers on lava flows. I have listed three other Nephrolepis species as present, one in 1951, the others in 1971. I have not been able to consult a specimen of N. tomentosa from anywhere, nor have I seen the Anak Krakatau collections of any of the four. So I cannot comment on the possibility that all of these records may be different identifications of the same species in this extremely difficult genus. Also quoted as occurring on ash-covered lava flows is Melastoma affinis. This may very probably be the same as what I have recorded as M. malabathricum L. sensu lato.

A definitive study of the flora and successional vegetation of Anak should include comparison of all of the actual specimens previously gathered there. In this way, only, can we be sure of how many and which species we are dealing with.

Appended are several lists that indicate changes in the Anak flora since the appearance of this new volcanic cone in 1930.

Species present previous to 1951:

Nephrolepis hirsutula
Hernandia sonora
Pityrogramma calomelanos
Thuarea involuta
Cycas circinalis
Antidesma sp.
Cerbera manghas
Cissus repens
Derris trifoliata
Murraya exotica
Musa paradisiaca
Nypa fruticans
Phaseolus sp.
Xylocarpus granatum
Vigna marina

Species present in 1963:

Canavalia rosea
Cassytha filiformis
Morinda citrifolia
Spinifex littoreus
Ipomoea pes-caprae ssp. *brasiliensis*
Pandanus tectorius
Remirea maritima
Ischaemum muticum
Cyperus javanicus
Fimbristylis cymosa
Chromolaena odorata
Imperata cylindrica
Saccharum spontaneum L. var. *klagha*
Ipomoea littoralis
Premna obtusifolia
Desmodium umbellatum
Erythrina variegata
Clerodendrum inerme
Casuarina equisetifolia
Terminalia catappa
Hibiscus tiliaceus
Pongamia pinnata
Calophyllum inophyllum
Barringtonia asiatica
Scaevola sericea

Species present in 1963 but not found in 1971:

Remirea maritima
Fimbristylis cymosa
Clerodendrum inerme

Species present in 1971, but not found in 1963:

Albizia retusa
Cerbera manghas
Cocos nucifera
Colubrina asiatica
Dodonaea viscosa
Eulophia pulchra
Euphorbia chamiissonis
Ficus fulva
Ficus septica
Guettarda speciosa
Lygodium flexuosum
Melastoma malabathricum
Nephrolepis falcata
Nephrolepis radicans
Piper aduncum

CHECKLIST OF THE HERPETOFAUNA OF THE MASCARENE ISLANDS

by D. D. Tirvengadam* and R. Bour**

ABSTRACT

An up to date checklist of the reptiles and amphibians of Mauritius, Rodrigues, Round Island and Reunion is presented. Maps showing subfossil collecting sites and localities where living specimens had been reported by old settlers, sailors, or travellers are also included.

RESUME

Une liste à jour des reptiles et amphibiens de l'Ile Maurice ainsi que de Rodrigues, de l'Ile Ronde et de la Réunion est présentée, et également des cartes précisant les sites de collecte de subfossiles et les endroits où ont été repérés des spécimens vivants par d'anciens colons, des marins, ou des voyageurs.

The small Mascarene islands, Mauritius, Rodrigues, Reunion and particularly Round Island, an offshore islet lying northeast of Mauritius, supported a poor but interesting and peculiar reptile fauna. Over the past three centuries with the advent of man followed by large settlement, the reptile populations of these islands, the endemic elements in particular, have suffered considerably from degradation of their natural habitats and from the depredation of domestic animals.

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Reports from various sources in Mauritius and Reunion and a survey carried out by the authors in Rodrigues and on Round Island in 1980 reveal that the composition of the reptile fauna have been greatly modified: impoverishment of the previously abundant endemic species, precarious existence on Round Island of the most remarkable representatives of the reptile fauna of the Mascarenes. There has also been a depletion of the introduced species (tortoises, frogs, agamids, snakes).

A reappraisal of all existing genera and species hitherto described permits the publication of a complete list of extant and extinct reptiles and amphibians of the Mascarene islands. A list of amphibians and reptiles erroneously cited in literature or accidentally met with in the Mascarene islands is also given.

ACKNOWLEDGEMENTS

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Mr. Roger Bour helped in setting up a permanent showcase on the reptile fauna of Mauritius and the neighbouring islands in the Natural History Museum of the Institute on the occasion of the centenary of the Mauritius Institute in November 1980.

TABLE 1 : List of species

	Mauritius	Round Island	Rodrigues	Réunion
LIZARDS				
Calotes versicolor (Daudin)	▲			▲
Chamaeleo pardalis (Cuvier)	△			☆
SKINKS				
Cryptoblepharus boutonii (Desjardins)	★	●		○
Gongylomorphus bojerii borbonica Vinson & Vinson	★	●		○
Leiopisma (= Didosaurus) mauritiana (Günther)	○			
Leiopisma telfairii (Desjardins)	○	●		○
DIURNAL GECKOS (Green lizards)				
Phelsuma borbonica agalegae Cheke	A	G A	L E G	A
Phelsuma borbonica borbonica Mertens				●
Phelsuma cepedianana (Milbert)	●			☆
Phelsuma edwardnewtonii Vinson & Vinson			○	
Phelsuma gigas (Liénard)			○	
Phelsuma guimbeaui Mertens *	●			
Phelsuma guentheri Boulenger		●		☆
Phelsuma lineata Gray				
Phelsuma ornata Gray (= vinsoni)				
subsp. ornata Gray	●	●		★
subsp. inexpectata Mertens (Réunion)				●
subsp. coindemirensis (Gunner's Quoin, Mauritius)	●			
* subsp. guimbeaui Mertens (Mauritius)				
subsp. roseigularis Vinson (Mauritius)				

	Mauritius	Round Island	Rodrigues	Reunion
NOCTURNAL LIZARDS ("Mabuyas")				
<i>Cyrtodactylus serpensis</i> (Loveridge)	○	★		
<i>Ebenavia inunguis</i> Boettger	▲			▲
<i>Gehyra mutilata</i> (Wiegmann)	▲		▲	▲
<i>Hemidactylus frenatus</i> Schlegel	▲		▲	▲
<i>Hemidactylus mabouia</i> (Moreau de Jonnès) (= <i>mercatorius</i>)	▲		☆	▲
<i>Hemiphyllodactylus typus</i> Bleeker	▲		▲	▲
<i>Lepidodactylus lugubris</i> Duméril et Bibron			▲	
FROG				
<i>Ptychoadena mascareniensis</i> mascareniensis (Duméril & Bibron)	▲			▲
TOADS				
<i>Bufo marinus</i> (Linne)	☆			
<i>Bufo gutturalis</i> Power	▲			▲
TORTOISES				
- <i>Lanz-Tortoises</i>				
<i>Astrochelys radiata</i> (Shaw)	?			☆
<i>Cylindraspis borbonica</i> Bour				○
<i>Cylindraspis graii</i> (Duméril et Bibron) (= <i>triserrata</i> ?)	○	○		
<i>Cylindraspis inepta</i> (Günther)	○	○		
<i>Cylindraspis peltastes</i> (Duméril et Bibron)			○	
<i>Cylindraspis vosmaeri</i> (Fitzinger)			○	
<i>Dipsochelys elephantina</i> (D. & B.) (= <i>Testudo gigantea</i>)	☆			☆
- <i>Fresh-Water Tortoises</i>				
<i>Pelusios subniger</i> (Lacépède)	△			
<i>Trionyx steindachneri</i> Siebenrock	▲			

- *Marine Turtles*

Chelonia mydas (Linné) (green turtle)
 Dermochelys coriacea (Vandelli) (lute)
 Eretmochelys imbricata (Linné) (Hawk's bill)

SNAKES

Bolyeria multocarinata (Boie) }
 Casarea dussumieri (Schegel) } (boa)
 Lycodon aulicus (Linné)
 Pelamis platurus (Linné) (sea-snake)
 Rhamphotyphlops braminus (Daudin) (blind snake)
 "Typhlops" cariei Hoffstetter

Mauritius	Round Island	Rodrigues	Réunion
★	★	●	★
★			
★	★	●	★
	★		
○	★		
▲	★		▲
★	★		▲
▲		▲	
○			

KEY TO SYMBOLS :

. Endemic species

● present

★ accidental, rare or localized

○ extinct

. Introduced species

▲ present

☆ rare or localized

△ extinct

AMPHIBIANS AND REPTILES ERRONEOUSLY CITED
OR ACCIDENTLY ENCOUNTERED IN THE MASCARENE ISLANDS

M = Mauritius

R = Reunion

Rodr. = Rodrigues

FROGS AND TOADS

- *Bufo melanostictus* R
- *Rana hexadactyla* R
- *Rana tigrina* R

CROCODILES

- *Crocodylus niloticus* M
- *Crocodylus porosus* M

TURTLES

- *Amyda cartilaginea* M
- *Chinemys reevesii* M
- *Chrysemys s. elegans* M, R
- *Cuora amboinensis* M
- *Dipsochelys elephantina* Rodr. ?
- *Geomyda spengleri* M, R
- *Homopus areolatus* M
- *Homopus signatus* M
- *Psammobates geometricus* M
- *Psammobates tentorius* M
- *Testudo graeca* Rodr.

SNAKES

- *Acrantophis dumerilii* M ?, R
- *Dromicodryas bernieri* M
- *Helmintophis flavoterminalis* M
- *Liophidium vaillantii* M
- *Praepeditus lineatus* M (an obscure name; the identity of this nominal species has not yet been clarified)

CHAMELEONS

- *Chamaeleo bifidus* M, R
- *Chamaeleo lateralis* R
- *Chamaeleo pardalis* M
- *Chamaeleo parsonii* M
- *Chamaeleo pumilus* M, R
- *Chamaeleo tigris* M, R
- *Chamaeleo verrucosus* M, R

REFERENCES

- Arnold, E.N. (1979). Indian Ocean giant tortoises : their systematics and island adaptations. Phil. Trans. R. Soc. Lond. (B) 286 : 127-145.
- Arnold, E.N. (1980). Recently extinct reptile populations from Mauritius and Reunion, Indian Ocean. J. Zool., Lond. 191 : 33-47.
- Bour, R. (1978). Les tortues des Mascareignes : description d'une espèce nouvelle d'après un document (Mémoires de l'Académie) de 1737 dans lequel le crâne est figuré. C.R. Acad. Sc. Paris (D) 287 : 491-493.
- Bour, R. (1979). Première découverte de restes osseux de la tortue terrestre de La Réunion, *Cylindraspis borbonica*. C.R. Acad. Sc. Paris (D) 228 : 1223-1226.
- Bour, R. (1980). Systématique des tortues terrestres des îles Mascareignes : genre *Cylindraspis* Fitzinger, 1835 (Reptilia, Chelonii). Bull. Mus. natn. Hist. nat. Paris, 4e sec., A, 3 : 895-904.
- Bour, R. (1980). Essai sur la taxinomie des Testudinidae actuels (Reptilia, Chelonii). Bull. Mus. natn. Hist. nat., Paris, 4e sér., A, 2 : 541-546.
- Bour, R. & F. Moutou (1982). Reptiles et amphibiens de l'île de la Réunion. Info-Nature, Ile de la Réunion, n° 19 : 119-156.
- Vinson, J. & Vinson, J.M. (1969). The saurian fauna of the Mascarene Islands. Bull. Mauritius Inst. 6 : 203-320.

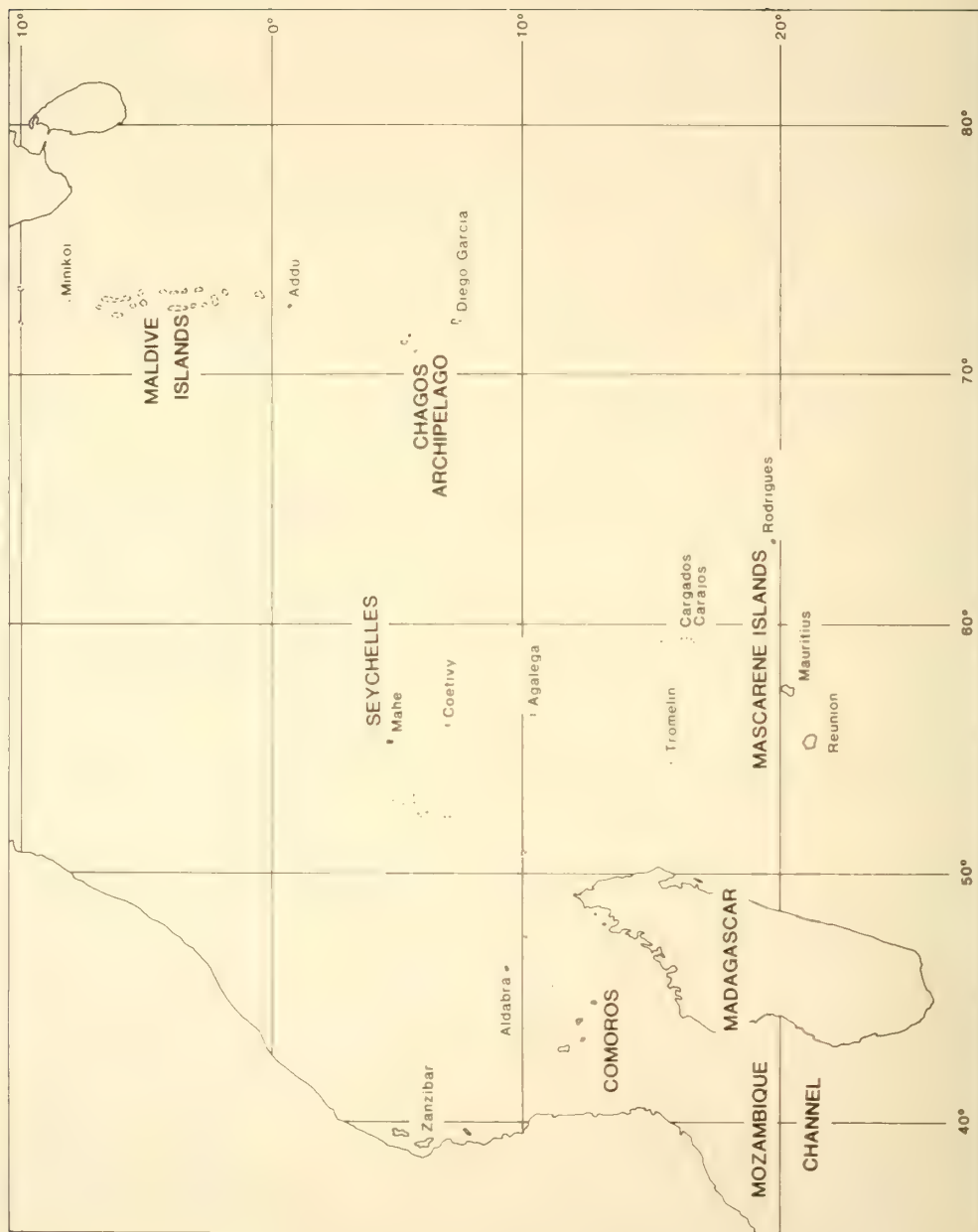
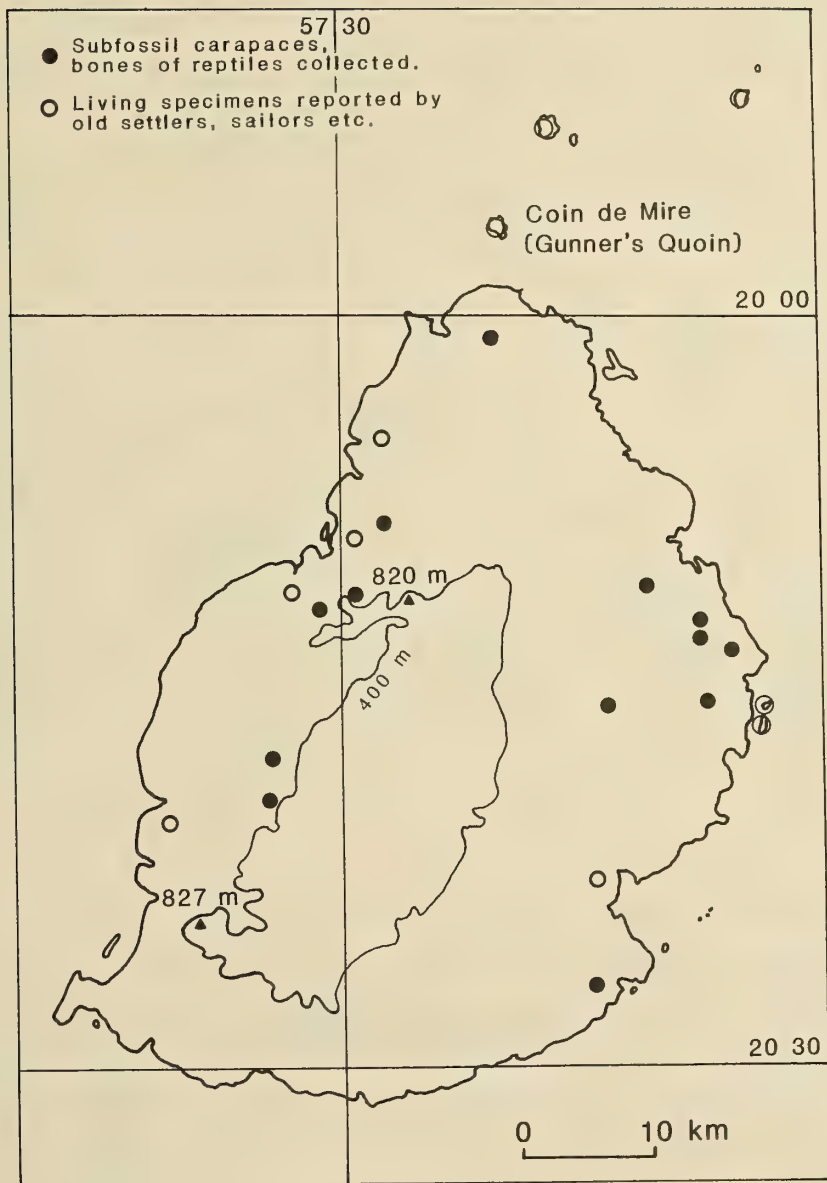
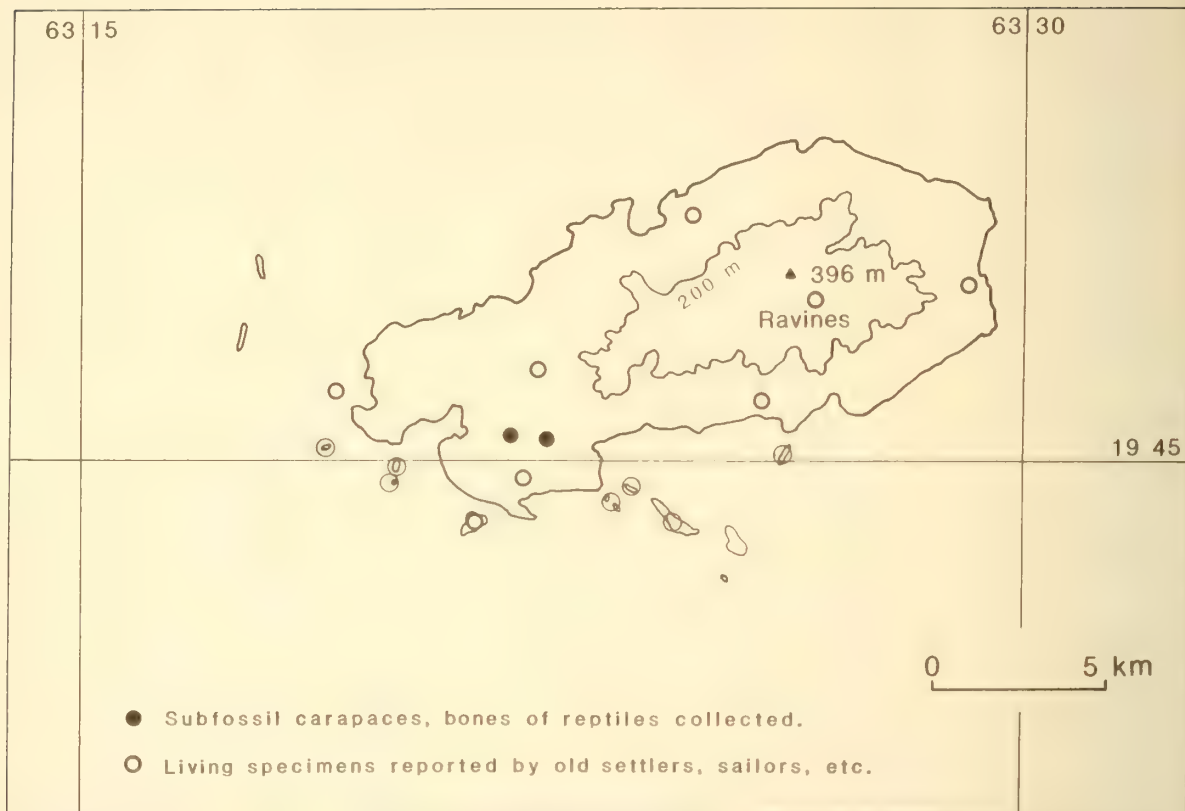


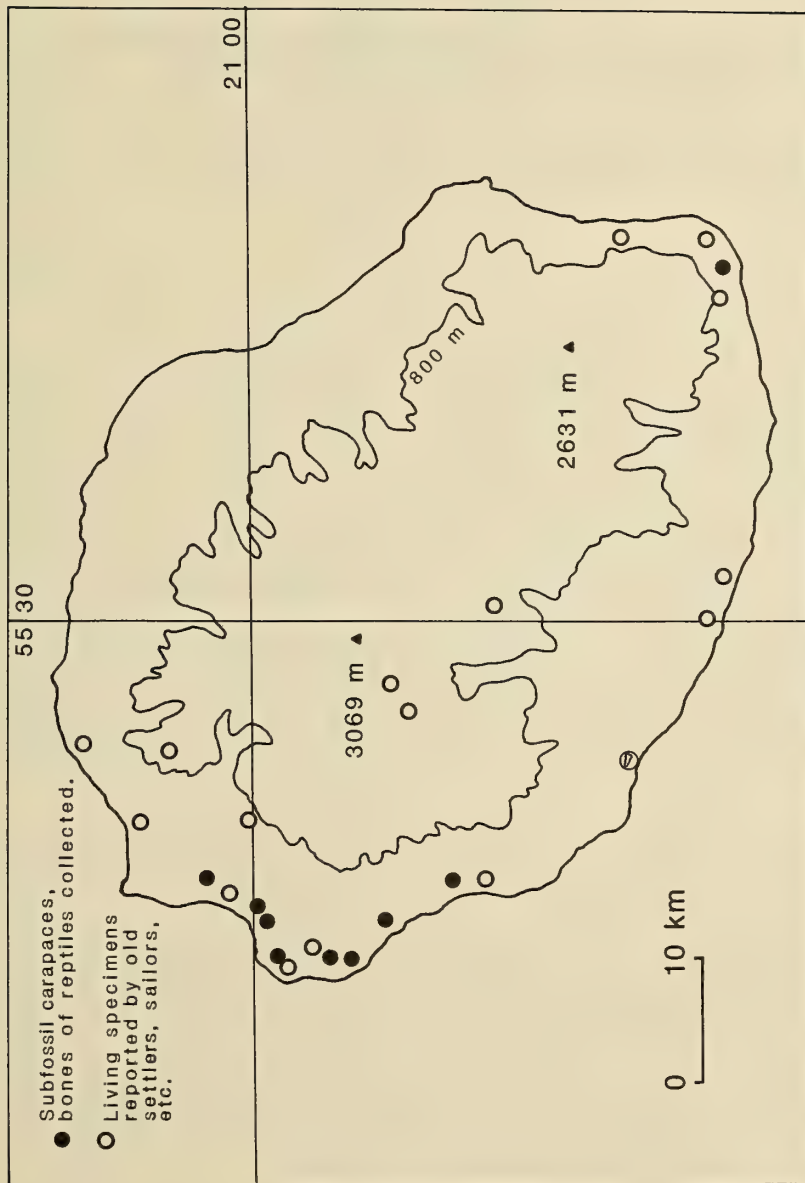
Fig. 1. Location of the Mascarene Islands in the Indian Ocean



MAURITIUS



RODRIGUES



REUNION

MARINE AND TERRESTRIAL FLORA AND FAUNA NOTES
ON SOMBRERO ISLAND IN THE CARIBBEAN

by Nancy B. Ogden, William G. Gladfelter
John C. Ogden and Elizabeth H. Gladfelter *

Introduction

Sombrero Island (Lat. 18° 36' N, Long. 63° 25' W; Fig. 1) is an elevated block of limestone 6-12 m above sea level with no beaches and a precarious anchorage subject to damaging ground swells. It is 1.2 km long and approaches the shape of an obtuse triangle extending northeast and southwest. Isolated from the Anguillan bank by the 32-mile Sombrero Passage, it forms the northernmost limit of the Lesser Antilles and is separated from the Puerto Rican/Virgin Islands bank (part of the Greater Antilles) by the 40-mile wide Anegada Passage. Sombrero is 366 m wide at its widest and represents a remnant of an island believed to have been as large as its present 5.6 x 8 km wide underwater platform which varies from 16-30 m deep. It is believed to consist of a volcanic base capped by Pleistocene limestone (Julien, 1866). According to Julien this limestone represents the floor of a pre-historic lagoon once protected by a barrier reef and possibly enclosed by an atoll. His evidence for this is the abundance of fossils, in particular, Bulla (bubble shell). The fossil shells and corals are extensively described by Julien.

Presently Sombrero is exposed to the open Atlantic Ocean. The occasional severe ground swells and regular heavy seas limit coral growth. They also affect the land-dwelling populations. Fortunately, the seas were calm for our stay, but even then the salt spray was evident. The eroded cliffs are precipitous (Fig. 2) and undercut, but occasionally slope toward the water and are then undercut below the water surface. The island was uninhabited until 1856 when operations began for mining of the phosphate rich, rock-guano deposits. Presently it is inhabited by four lighthouse keepers.

The following observations were made on June 10-11, 1979 using the yacht Tüchtig.

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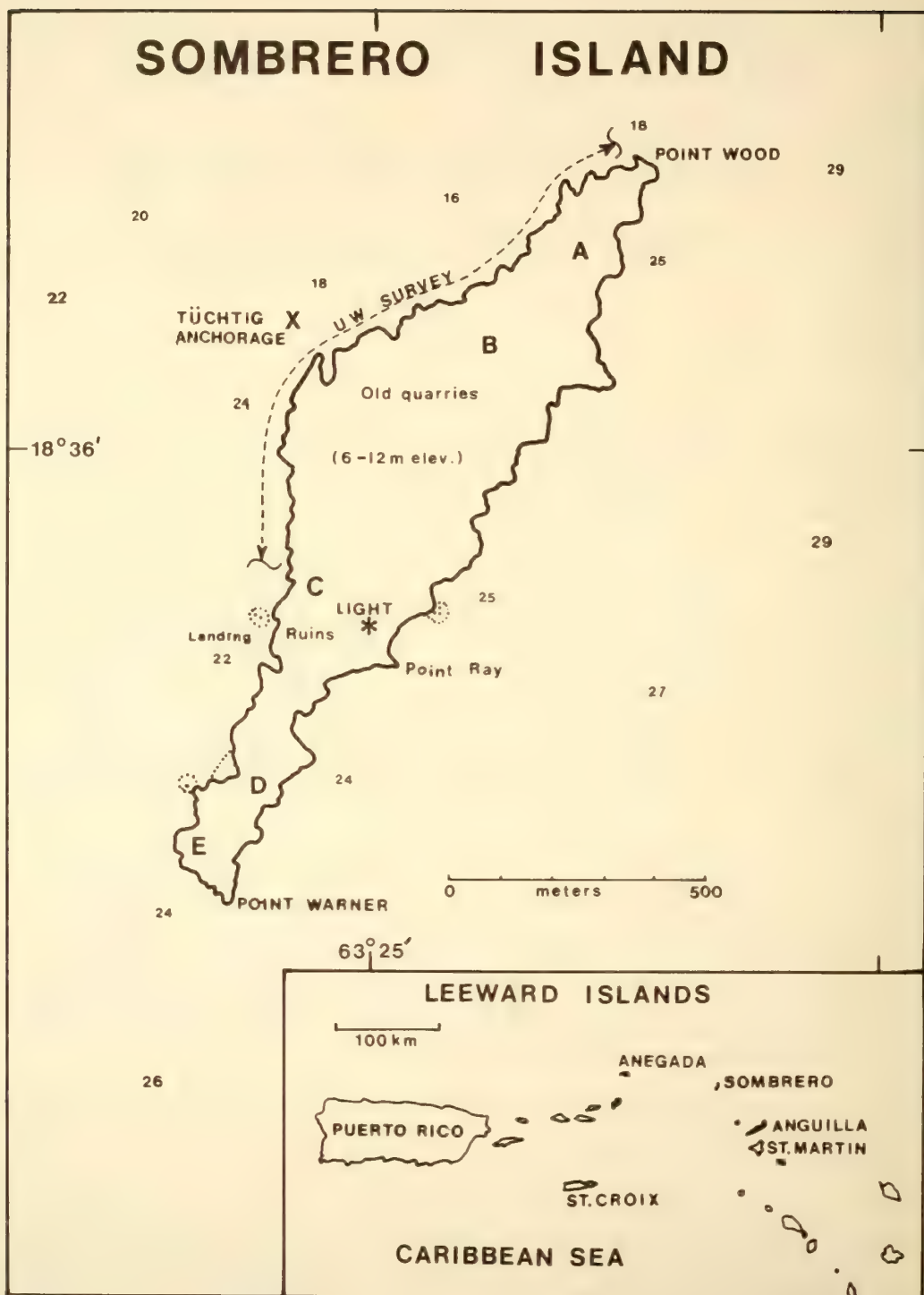


Fig. 1. Sombrero Is. (DMA, 1976) with an inset of its location in the Eastern Caribbean island chain; depths in meters; dotted line shows extent of the underwater survey. A-E represents bird areas listed in Table 2.

Land Plants

One's first impression is that there are only two species of land plants, but walking the length of the island and back revealed 8 species (Table 1). Pluchea symphytifolium (grows to 3 m tall) must be a recent introduction as previous literature refers to the cactus Opuntia antillana (grows to 0.6 m tall) as the tallest plant on the island. The most abundant plant, sea purslane (Sesuvium portulacastrum), appeared to be the preferred nesting site for boobies (Fig. 4) while blast holes, rock rubble, crevices and natural depressions provided numerous niches for the other six species of nesting sea birds.

Birds

Seabirds arrive from the south in March and depart in late May, June, July and even August (Lawrence, 1864). "The lighthouse crew" (during phosphate mining years) "reports that nests and eggs can be found on the island during at least 8 months of the year" (Lawrence, 1864). According to Lawrence, the nesting seabirds suffered considerably from poaching by the phosphate miners. Quarrying of the guano deposits went on from 1856 (Lawrence, 1864) to 1890. Julien arrived in 1860 and four years later made the statement that "... laborers have been so indefatigable that I do not believe a single young bird has been hatched since our occupation of the Key. Consequently, last season (spring of 1863) only about two dozen eggs in all were found, instead of the thousands of previous years." Julien also mentioned wild cats as predators (Lawrence, 1864). We suspect the nesting bird populations have recovered considerably since then, but according to the present head lighthouse keeper, men still come from Anguilla to get eggs and birds. Migrating birds sometimes appear on the island and occasionally birds from larger neighboring islands (Lawrence, 1864). We observed nests of noddy, sooty and bridled terns and brown boobies. Julien never saw booby nests despite their presence from June to November - suggesting the thorough poaching of their eggs. Lazell (1964) did see them nesting. Noddy terns were most abundant of all, as was the case during Julien's stay (Table 2).

Reptiles

Other than the seven species of nesting birds, the black lizard Amieva corvina (Teiidae) is the next most obvious inhabitant. This endemic, slatey black or black and tan (occasionally with light speckled flanks) lizard was the only recorded living reptile until 1964. We observed it throughout the island. Its main food is reported to be bird's eggs (Lazell, 1964). One was observed during our stay eating the small, yellow Portulaca flowers. Lazell (1964) reported the lizard Anolis gingivinus (Iguanidae) and the gecko Sphaerodactylus sputator (Gekkonidae) - both are common to the Anguillan and St. Kitts banks. Only one Anolis was seen in the north central portion of the island during our visit. According to Lazell (1964) the Anolis varies from olive drab to distinctly light greenish with a bold, light flank stripe and varying spots. The gecko is "at or near the longitudinally-striped, extreme color pattern" (Lazell, 1964). It was not seen by us.

Julien (1866) mentions the discovery of fossil remains of land turtles which he was led to believe belonged to three new extinct and gigantic species similar to those of the Galapagos Islands. Auffenberg (1967) finds that none of Julien's original fragments can be found, but he and a colleague obtained more in the Pleistocene fissures at the northern end of Sombrero in 1964. Auffenberg (1967) states that Julien's tortoise fragments were originally described as the new species Emys sombreroensis Leidy. It is now known as Geochelone sombreroensis (Leidy) Auffenberg, 1967. The sternum length was hypothesized to have been 12 inches. Some of Julien's material reportedly represented specimens with a plastral length of at least 32 inches (Auff. 1967). Geochelone carbonaria (Spix) Morocoy is a species presently found on many Caribbean Islands. It is commonly around 12 inches in length, but larger ones have been reported (pers. com.). G. denticulata (Linnaeus) which has reached a shell length of 26.5 inches is reportedly found in Trinidad (Underwood, 1962).

Marine Algae

The marine algae on the exposed limestone cliffs were quite different from other Caribbean islands. Wrangelia penicillata, commonly found 2 m deep and deeper, was the most common macroalga in the splash zone for 2 m above the surface. Also there was a surprising lack of Sargassum and Turbinaria at the surface. Protected areas were more typical of combinations found elsewhere. In general brown algae - Dictyopteris delicatula; Dictyota dichotoma, D. dentata and Lobophora variegata represented the most biomass 2 m deep and below. Four species of colorful, fleshy, encrusting algae were very striking in the top two meters. Snorkelling and scuba diving were limited to the northern half of the leeward side (Fig. 1), while collections were made from land on the windward side of the northeast end (Table 3).

Coral

There were no reef-like accumulations of coral, but the species common on other eastern Caribbean islands were generally well represented particularly on the shelf on the northern side of the island. Colonies were generally of moderate size and flattened, especially on the vertical slopes of the island. Coral growth must be affected by the occasional severe ground swells that toss boulders and cobbles about on the bottom and have cut a notch at the base of the island at a depth of about 10 m.

Fishes

The fish community generally was rich and diverse (Table 4). A few species unusually well represented were Kyphosus sectatrix (Bermuda chub) and Cephalopholis fulva (coney) - common near the walls; and Paranthias furcifer (Creole fish) and Xanthichthys ringeas (Sargassum triggerfish) common over the leeward shelf. Conspicuous by their absence were grunts, probably due to the lack of soft bottom and seagrass beds. The proportional representation of major trophic categories (Table 5) was similar

to shelf edge fish communities censused elsewhere in the northeastern Caribbean by the authors (unpublished).

Miscellaneous Observations

A colorful variation of the crab Grapsus can be seen skirting the edges of the island. The periphery of the island is dotted with salt-water, brackish and fresh water pools. Seven meters above the sea level there were pools with occasional ocean surgeonfish, sergeant majors and Diadema (the long-spined black sea urchin). Echinometra, a short-spined urchin, inhabited the wave-washed areas. Some pools were choked with filamentous, green algae. Others had waterbugs, backswimmers, and other small swimming organisms.

Insects, in general, were not noted, but houseflies, a flattened, tan spider, the cabbage butterfly, red mites and small elongate ants were observed. Tectarius shells seemed poor fare for the purple-clawed hermit crab Coenobita clypeatus which grows much larger on other islands where larger shells are available. In general, other than sea birds, terrestrial life is very limited - probably due to the lack of soil and the presence of abundant salt spray.

Acknowledgements

Thanks are due to Dr. Michael Wynne of the University of Michigan for help with a few of the algae. Dr. Edward Towle of Island Resources Foundation generously provided us with the reprints and a map of Sombrero Island. Dr. F. Raymond Fosberg of Smithsonian looked over the land plant collection and encouraged this report. This is Contribution No. 124 of the West Indies Laboratory.

Bibliography

- Auffenberg, W. S. 1967. Notes on West Indian Tortoises. *Herpetologica* 23: 34-44.
- Defense Mapping Agency 1976. Anguilla to St. Christopher. Hydrographic Center, Wash. D.C. 20390. Chart No. 25606.
- Dickson, Hanmer (Ms.). Sombrero Island (history acquired from the lighthouse keeper).
- Julien, A. A. 1866. XXXI. On the Geology of the Key of Sombrero, W. I. *Ann. Lyceum Natural History* 8: 251-278.
- Lawrence, G. N. 1864. VIII. Catalogue of Birds Collected at the Island of Sombrero, W.I., with Observations by A. A. Julien. *Ann. Lyceum Natural History* 8: 92-106.
- Lazell, J. D. Jr. 1964. The Reptiles of Sombrero, West Indies. *Copeia* 4: 716-718.
- Underwood, Garth 1962. Reptiles of the Eastern Caribbean. Dept. of Extra-Mural Studies, University of the West Indies, Trinidad. *Carib. Affairs* No. 1: 192 pp.



Fig. 2. Looking north at the lighthouse near Pt. Ray; windward side on a calm day showing precipitous nature of the island's shoreline.



Fig. 3. Quarry area near our anchorage looking south toward the lighthouse.



Fig. 4. Area A (Fig. 1) with nesting brown boobies on the predominant island vegetation (Sesuvium portulacastrum); bridled tern also present.

TABLE I

LAND PLANTS

Listed in order of apparent abundance

Sesuvium portulacastrum (L.) L., Aizoaceae - trailing succulent with light pink flowers; the most common plant on the island and possibly eaten by Amieva.

Euphorbia mesembrianthemifolia (Chamasyce buxifolia) Jacq., Euphorbiaceae - bushy, yellow-stemmed (basally woody) plant to 50 cm tall with small, ovate, vaguely succulent leaves in two ranks (the leaves strikingly angled); the second most common plant on the island.

Heliotropium curassavicum L., Boraginaceae - bushy, trailing plant with somewhat succulent, frosted looking leaves with small white flowers in a typical scorpioid spike; branches grow to 15-45 cm long; fairly common in moist, protected areas on the southern end.

Portulaca oleracea L., Portulacaceae - low, somewhat succulent herb found in an isolated patch; Amieva was observed eating the small yellow flowers.

Euphorbia serpens H.B.K., Euphorbiaceae - fragile, pink-stemmed, trailing herb with small ovate leaves; found with Portulaca.

Opuntia antillana Britton & Rose, Cactaceae - yellow-flowering cactus with 3-6 coarse, yellow spines; grows to 0.6 m tall; found isolated and locally abundant in a large, sloping pit.

Fimbristylis cymosa Roth, Cyperaceae - a low sedge somewhat 2-ranked at the base; blades slightly cupped basally; spikelets 3 mm long; found between the lighthouse and the landing.

Pluchea symphytifolium (Mill) Gillis, Compositae - a bush to 3 m tall with large, lanceolate leaves that smell like horse liniment; two bushes seen in the sandy area N.E. of the buildings; probably a recent introduction.

TABLE 2

**BIRDS: Comparative observations of
Julien (Lawrence 1864) appear in parentheses**

Refer to Fig. 1 for lettered areas

- Noddy tern (Anous stolidus) - nesting throughout in caves and crevices; 100 birds seen on nests; one egg per nest; probably 500 nests on the island (Julien describes the nest-building process); birds are aggressive.
- Sooty tern (Sterna fuscata) - some nesting, mostly not (?); concentrated in area north of the lighthouse; about 100 birds total (associate with noddies). Area B.
- Bridled tern (S. anaethetus) - mostly south of the lighthouse; some nesting; more common than sooty terns; probably several hundred birds total; many dead and sick among the rocks (Julien suggests it to have been the most abundant bird next to the noddies and royal terns; lays one* egg). * We saw up to three eggs per nest. Area D.
- Roseate tern (S. dougallii) - one main colony in the south - a "grassy" area; not nesting, but probably do; a few were observed roosting on tailings mid-island; about 30-40 total. Area E.
- Least tern (S. albifrons) - main concentration in the center of the island in a flat, pebbly area; no sign of breeding, but probably do; 20-30 birds total. Area C.
- Royal tern (Thalasseus maximus) - one pair observed arriving in the evening and departing in the morning (nested in June; departed in August; present in variable numbers; disappearing during the day or for weeks).
- Tropicbird (Phaeton sp.) - one seen overhead in the evening. (Julien saw one nest and small numbers of P. aethereus, but suggests they were abundant previous to mining years. He also described seeing one other species).
- Laughing gull (Larus atricilla) - common on leeward bluffs (not abundant during Julien's stay; associating with the royal terns.)
- Frigatebird (Fregata magnificens) - common (breed June - July).
- Brown Booby (Sula leucogaster) - nesting at northern tip of the island; eggs and large young present; about 30 nests (?); roost on leeward rocks and off south end of island; about 60 birds total. Area A. (Fig. 4).
- Ruddy turnstone (Arenaria interpres) - 1 pair seen at several sites on the island (small numbers present November - May).
- Cattle egret (Bubulcus ibis) - 7 in the vicinity of the lighthouse.

TABLE 3
MARINE ALGAE

Rhodophyta (red algae)

- Amphiroa sp. (N1144) 0.5 m deep, small inlet
Botryocladia sp. 16 m deep
Callithamnion herveyi (N1142, N1177) uncommon, 1.5 m deep in small inlet and 5 m deep on wall.
Centroceras clavulatum (N1185) splash zone
Ceramium byssoideum (on N1143, N1169 & N1185) splash zone to 1.5 m deep.
Champia parvula (on N1151) 13 m deep
Chondria sp. (erect on N1151) 13 m deep
Chondria sp. (creeping on N1151) 13 m deep
Corallina subulata (N1154) 14 m deep
 Crustose coralline cobbles (unidentified) 16 m deep
Gelidium pusillum 16 m deep
Griffithsia sp. (on N1151) 13 m deep
Grallatoria reptans (N1173) abundant exposed and to 1 m deep
Halymenia pseudofloresia (N1146, N1170, N1153) 5-16 m. had a striking bright orange on brown reticulation which turned plain rose-colored upon preservation.
Herposiphonia pecten-veneris (N1176) 16 m deep
Hypnea sp. 16 m deep
Hypoglossum tenuifolium V. carolinianum (on N1151 & N1154) 13 m deep
Jania adherans (with Amphiroa N1144) 0.5 m deep
Jania capillacea (on Laurencia obtusa N1143) 1 m deep
Laurencia intricata (N1160, N1145) 1 m & less in inlet and splash zone.
Laurencia obtusa (N1143, N1169) scattered to abundant - surface to 1.5 m deep
Laurencia papillosa (N1183) exposed in splash zone
Liagora valida (N1180) 14 m deep
Lophosiphonia sp. splash zone
Martensia pavonia (on N1151) 13 m deep, also seen protected near the surface.
Polysiphonia sp. (N1176) from Colpomenia 16 m deep
Taenioma purpusillum (N1185) splash zone
Wrangelia argus seen at the surface
Wrangelia pencillata (N1171, N1145) 1-2 m above the surface dominating a 1 m wide band in the splash zone
 3 unidentified fleshy crusts - bright orange (most abundant), rose-pink and chocolate purple; very dominant from the surface to 2 m deep.
 Unidentified polysiphonous red - 16 m deep, creeping on Lobophora (N1173)

Phaeophyta (brown algae)

- Colpomenia sinuosa (N1179) 16 m deep, small plants
Dictyopteris delicatula (N1165, N1148) the most dominant alga from 2-3 m deep, but also found at 14 m deep.
Dictyota bartayresii (N1168) 14 m deep
D. ciliolata (N1182) 14 m deep

Phaeophyta (brown algae) continued

- D. dentata (N1167) scattered to abundant several meters deep; also abundant 9 - 14 m deep.
D. dichotoma (N1147) very abundant 9-16 m deep
D. divaricata (N1182) 16 m deep
D. sp. (N1164) 16 m deep
Dilophus alternans (N1166) 16 m deep, stunted
Lobophora variegata (with N1154) (N1163) abundant 16 m deep; common as a crust in shallow water and exposed.
Padina sp. (N1178) 16 m deep, scarce
Sargassum polyceratum (N1141) scattered or locally abundant, 1 m deep to exposed.
Sargassum sp. (N1162) 9 m deep on wall
Sphacelaria sp. (N1176) 16 m deep
Stypopodium zonale (N1161) small plant 16 m deep
Turbinaria turbinata (N1140) scattered, surface to exposed.

Chlorophyta (green algae)

- Acetabularia sp. 16 m deep
Anadyomene stellata (N1149) abundant on parts of the wall 5-8 m deep
Avrainvillea nigricans (N1150) 13 m deep
Bryopsis plumosa abundant in one inlet at the surface
Caulerpa microphysa (N1155) 1.5 m and 14 m deep
Caulerpa vickersiae 16 m deep
Cladophora sp. in tide pool
Halimeda discoidea (N1152) 13 m deep
Halimeda tuna (N1151) 13 m deep
Neomeris annulata scattered 16 m deep
Rhipiliopsis stri (N1176) on wall 8 m deep
N1174 unidentified long skeins of very fine green filaments (17 μ diam); spray zone tide pool.
N1175 unidentified, branched, tangled, filamentous green 8 cm tall; spray zone tide pool.

Cyanophyta (bluegreen algae)

- Trichodesmium thiebautii (N1186) quite common; planktonic
N1181
N1184
Oscillatoria sp. (N1176) common on wall

TABLE 4

FISHES

Feeding and Abundance Categories (Sombrero Island,
Northern Half of Leeward Side)

Feeding Category Key:

C = Crustaceavore
P = Planktivore
F = Piscivore
H = Herbivore
G = Invertebrate Generalist
S = Invertebrate Specialist

Abundance Category Key:

1 = 0-1/hr.
2 = 1-2 hr.
3 = 2-5
4 = 5-10
5 = 10-25
6 = 25-30
7 = 50

C	3	<u>Holocentrus rufus</u> (squirrelfish) - mainly in boulder strewn cove.
C	5	<u>H. ascensionis</u> (longjaw squirrelfish) - base of wall; more common toward the seaward end.
C	3	<u>Adioryx vexillarius</u> (dusky squirrelfish) - among boulders in cove.
C	1	<u>A. coruscus</u> (reef squirrelfish) - base of leeward wall.
C	3	<u>Flammeo marianus</u> (longspine squirrelfish) - base of cliffs.
P	4	<u>Myripristis jacobus</u> (blackbar soldierfish) - boulders in cove.
P	3	<u>Priacanthus cruentatus</u> (glasseye snapper) - boulders in cove.
F	5	<u>Lutjanus apodus</u> (schoolmaster) - in schools on reef flats and near cliff base at seaward end.
F	2	<u>Mycteroperca venenosa</u> (yellowfin grouper) - large, near base of wall and out on reef flats.
F	2	<u>M. tigris</u> (tiger grouper) - large, at cliff base.
F	1	<u>Epinephelus adscensionis</u> (rock hind) - boulders in cove.
F	1	<u>E. striatus</u> (Nassau grouper) - under ledge near second mooring.
F	6	<u>Cephalopholis fulva</u> (coney) - along walls, base of walls and rubble.
P	6	<u>Paranthias furcifer</u> (creole fish) - over reef flats and south end of wall.
P	5	<u>Grama loreto</u> (fairy basslet) - under ledges
C	2	<u>Serranus tigrinus</u> (harlequin bass) - rubble at base of cliffs.
F	2	<u>Caranx latus</u> (horse-eye jack) - over sand, south end of swim; chasing mackerel scads.
F	5	<u>C. ruber</u> (bar jack) - in water column near moorings.
P	6	<u>Decapterus macarellus</u> (mackerel scad) - in a few schools above reef flats.
F	2	<u>Seriola rivoliana</u> (almaco jack) - same as horse-eye jack.
F	4	<u>Sphyræna barracuda</u> (great barracuda) - along walls and over reef flats.

FISHES (continued)

H	5-6	<u>Kyphosus sectatrix</u> (Bermuda chub) - cliffs, base of cliffs and over reef flats.
P	4-5	<u>Hemiramphus balao</u> (balao) - near surface at first mooring.
F	1	<u>Gymnothorax</u> sp. (moray)
G	4	<u>Malacanthus plumieri</u> (sand tilefish) - sand and rubble areas.
G	4	<u>Mulloidichthys martinicus</u> (yellow goatfish) - one group in boulders of cove.
G	3	<u>Pseudupeneus maculatus</u> (spotted goatfish) - small junction of reef flats and sand.
G	1	<u>Calamus</u> sp. (porgy) - over sand flats
C	3	<u>Amblycirrhitis pinos</u> (redspotted hawkfish) - sides and base of wall.
C	1	<u>Equetus punctatus</u> (spotted drum)
S	2	<u>Holacanthus ciliaris</u> (queen angelfish) - cliff base and walls at seaward end.
S	3	<u>H. tricolor</u> (rock beauty) - cliff base and outer (seaward) reef flats.
S	2	<u>Pomacanthus arcuatus</u> (grey angelfish) - one pair in shallow sand-bottom cove.
S	2	<u>P. paru</u> (French angelfish) - reef flats and cliff base at seaward end.
H	5	<u>Eupomacentrus dorsopunicans</u> (dusky damselfish) - juveniles common on walls.
G	5	<u>E. partitus</u> (bicolor damselfish) - common on deeper reef flats near seaward end.
H	2	<u>Microspathodon chrysurus</u> (yellowtail damselfish) - boulders in cove.
G,P	5-6	<u>Abudefduf saxatilis</u> (sergeant major) - inshore.
G	2	<u>Chaetodon striatus</u> (banded butterflyfish) - cliff base and walls at seaward end.
P	5-6	<u>Chromis cyanea</u> (blue chromis) - reef flats and cliffs at seaward end.
P	5-6	<u>C. multilineata</u> (brown chromis) - cliffs
P,G	6-7	<u>Thalassoma bifasciatum</u> (bluehead) - common
G	2	<u>Halichoeres bivittatus</u> (slippery dick) - sand and reef flats.
G	4	<u>H. garnoti</u> (yellowhead wrasse) - cliff base, especially the seaward end.
G	3	<u>H. maculipinna</u> (clown wrasse) - cliff base.
G	2	<u>H. radiatus</u> (puddingwife) - cliff base
P	5	<u>Clepticus parrai</u> (creole wrasse) - water column above reef flats.
G	5	<u>Bodianus rufus</u> (Spanish hogfish) - small to large along cliffs and cliff bases.
H	2	<u>Scarus coelestinus</u> (midnight parrotfish) - reef flats.
H	4	<u>S. croicensis</u> (striped parrotfish) - cliff base especially the seaward end.
H	4-5	<u>S. vetula</u> (queen parrotfish) - cliff sides and bases
H	2	<u>Sparisoma aurofrenatum</u> (redband parrotfish) - cliff sides and bases.

FISHES (continued)

H	3	<u>S. chrysopterus</u> (redtail parrotfish) - cliff base.
H	1	<u>S. rubripinne</u> (yellowtail parrotfish) - reef base.
H	4-5	<u>S. viride</u> (stoplight parrotfish) - cliff sides and bases.
H	5	<u>Ophioblennius atlanticus</u> (redlip blenny) - cliff sides
H	3	<u>Bathygobius</u> sp. (goby) - splash zones on the north end.
H	4-5	<u>Acanthurus bahianus</u> (ocean surgeon)
H	4	<u>A. chirurgus</u> (doctorfish) - seaward reef flats
H	6-7	<u>A. coerulens</u> (bluetang) - cliffs.
S	3	<u>Balistes vetula</u> (queen triggerfish) - over reef flats.
P?	5	<u>Xanthichthys ringens</u> (Sargassum triggerfish) - over reef flats and in water column.
H	4-5	<u>Melichthys niger</u> (black durgon) - over reef flats at moorings.
G	2	<u>Cantherhines macrocerus</u> (whitespotted filefish) - large, at cliff base.
G	2	<u>C. pullus</u> (orangespotted filefish) - cliffs.
G	1	<u>Alutera scripta</u> (scrawled filefish) - cliffs.
G	2	<u>Lactophrys bicaudalis</u> (spotted trunkfish) - cliff base.
G	2	<u>L. triqueter</u> (smooth trunkfish) - cliff base
G	1	<u>Diodon hystrix</u> (porcupinefish) - cliff base in a cave.

TABLE 5

Summary of Abundances of Fish Feeding Guilds

Feeding Category	Symbol	No. spp. per Category	% of Total No. of Species	Category Abundances	% of Total Fish Seen
Herbivores	H	16	24	59	26
Invertebrate generalists	G	18	26	51	23
Invertebrate specialists	S	5	7	12	5
Crustaceavores	C	8	12	21	9
Piscivores	F	11	16	31	14
Planktivores	P	<u>10</u>	15	<u>50</u>	22
Total		68		224	

VEGETATION AND FLORA OF THE LOWENDAL ISLANDS, WESTERN AUSTRALIA

by Ralf Buckley

The Lowendal Islands are a group of small limestone islands between Barrow Island and the adjacent mainland of north western Western Australia (Figure 1). They lie between 20°34'30"S and 20°41'11"S and between 115°30'17"E and 115°34'43"E. Since the islands do not have individual names, they are designated by letters in Fig.1. They comprise eroded remnants of Pleistocene reefs, with caps, dunes or beaches of Holocene calcareous sand in some cases. In area, they range from bare pinnacles of a few hundred square metres or less to a relatively complex island of 0.77 km². This is named island B in Figure 1: no particular significance attaches to the order of naming. There are two main limestone terraces, the lower presumably of Holocene age: their precise elevations above mean sea level have not been ascertained. The climate corresponds to that of Barrow Island (Buckley 1983): a monsoonal climate with mean annual rainfall 200 mm, peaking in February-March and May-June. The only previous botanical record for the Lowendal islands appears to be that of Serventy and Marshall (1964), who recorded five species, namely Ptilotus exaltatus, Scaevola spinescens, Myoporum acuminatum, Spinifex longifolius and Triodia sp. from "Lowendall Island", presumably island B of Fig.1, in September 1958.

According to Serventy and Marshall (1964), "Lowendall Island" was named by the French Baudin expedition in March 1803. The official account of the expedition made no mention of the island's natural history, and it appears that Serventy and Marshall were in fact the first naturalists to visit the main island, and Mr W.H. Butler and myself the first to visit the smaller islands. The British atomic weapons expedition in 1952 visited the island, but it is not included in the resulting natural history report by Hill (1955). Serventy and Marshall (1964) described the main island as follows: "The island has a more picturesque appearance than Barrow Island, with a higher and steeper coastline and an attractive beach on the east side which affords an easy landing. Much of the island is of "pipey" bare limestone but there are vegetated depressions of deep red-brown soil. Dunes of white sand have built up at the north end. The flora of the island has not the barren aspect that characterises Barrow Island". The main aim of their visit was to record the fauna. They found two reptile species, namely Physignathus gilberti and Varanus sp.; no mammals, despite a nocturnal search for likely species; and 16 bird species, listed in Table 1. Only the first and last of the bird species listed were recorded as nesting.

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The vegetation of the nearby and much larger Barrow Island (233 km² in area), was mapped and described by Buckley (1983) in terms of 7 main vegetation types and 29 subtypes. Five of these subtypes occur on the Lowendal Islands, as follows.

Type 4: Coastal sand assemblages

Subtype 4a: strandline assemblage; characterised by Ipomoea pescaprae and Salsola kali.

Subtype 4b: white aeolian foredune areas: open vegetation dominated by Spinifex longifolius and also characterised by Ptilotus villosiflorus and Cynanchum floribundum.

Type 5: Coastal rock assemblages

Subtype 5a: limestone or conglomerate cliffs, scarps and headlands bearing Triodia wiseana, and also characterised by Sarcostemma australe and Capparis spinosa.

Subtype 5b: low limestone areas bearing Frankenia, Sclerolaena, Neobassia and Halosarcia species.

Type 6: Mangroves

Subtype 6b: old stands of Avicennia marina swamped by sand, with ground cover of halophytes toward inland margin: Neobassia astrocarpa, Sclerolaena spinosa, Halosarcia spp., Frankenia pauciflora, Threlkeldia diffusa, Enchylaena tomentosa and Sporobolus virginicus.

On the Lowendal Islands, the primary substrate and vegetation division is between limestone and sand. Limestone areas, which correspond approximately to the coastal rock assemblages on Barrow Island (vegetation types 5a and 5e of Buckley 1983) may be subdivided into low terrace, high terrace cliff-tops, and in the larger islands, high terrace areas further from the sea. The vegetation of white sands corresponds approximately to the coastal sand assemblages on Barrow Island (vegetation types 4a, 4b), and may be divided into beaches, small dunes, and thin caps over limestone. There are also stands of the mangrove Avicennia marina (type 6b) on several islands.

The plants present on 12 of the islands were recorded during visits in September 1980; these records are summarised in Table 2. Collections are held in the West Australian Herbarium, Perth. Island biogeographical interpretations are given by Buckley (1982). The overall flora is a subset of the Barrow Island flora, with the addition of six species not recorded from Barrow Island itself: Capparis sp. (RB 7155), Crotalaria medicaginea, Dicladanthera forrestii, Launaea sarmentosa, Lawrenzia sp. (RB 7137), and the unidentified sterile species RB 7144 (*Dolichandrone* sp.?).

Additional differences from corresponding Barrow Island vegetation types include the following. Firstly, the showy pink-flowered Ptilotus exaltatus is conspicuous on the higher limestone terraces of the Lowendal Islands but extremely scarce on Barrow Island, even in directly comparable habitats. Its abundance on the Lowendal Islands, which was also noted for the largest island by Serventy and Marshall (1964), is perhaps due to the absence of herbivorous macropods, which might also account for the greater frequency of Sesuvium portulacastrum, Tribulus cistoides, Atriplex semilunaris, Setaria dielsii, Commelina ensifolia, Ipomoea pes-caprae, Indigofera trita and Portulaca intraterranea on the Lowendal Islands (Buckley 1983).

Secondly, individuals of Nicotiana occidentalis, Chamaesyce australis, Calandrinia balonensis and Portulaca intraterranea on the Lowendal Islands are more succulent than those on Barrow Island or the mainland: this might be due to greater salinity, lower grazing pressure or the greater frequency of seabird colonies with associated disturbance and input of nitrogen and phosphorus.

Thirdly, defoliation of Capparis spinosa by Caper White butterfly larvae is more severe on the Lowendal Islands than on Barrow Island or the mainland. On such small islands, the relative magnitude of fluctuations in the host and herbivore populations may be greater, with 1980 perhaps a year when the herbivore/host ratio was high.

Fourthly, the mangrove patches on island A and one of the patches on island C (Fig.1) are now isolated from the sea by extensive sand barriers, and the individual plants are all large trees, their trunks partially sand-swamped. Since Avicennia marina seedlings establish only in tidal mud, this indicates that the sand barriers formed after the Avicennia populations established. It is possible that mature Avicennia trees cut off from the sea by a sand barrier could still propagate from seedlings whilst a mud patch remained around the roots, fed with seawater by percolation through the sand, but once the mud was swamped with sand further seedling establishment would be very unlikely. Hence an age on the mangroves would give a minimum age for the sand barriers. Such an age would be obtainable by radiocarbon dating if possible anomalies due to the past detonation of atomic bombs on the nearby Montebello Islands could be assessed and allowed for.

ACKNOWLEDGEMENTS

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REFERENCES

- Buckley, R.C., 1982. The habitat unit model of island biogeography. J. Biogeog., 9, 339-344.
- Buckley, R.C., 1983. The flora and vegetation of Barrow Island. J. Roy. Soc. West. Aust. 66, 91-105.
- Hill, F.L. 1955. Notes on the natural history of the Monte Bello Islands. Proc. Linn. Soc. Lond., 165, 113-124.
- Serventy, D.L., and Marshall, A.J., 1964. A natural history reconnaissance of Barrow and Montebello Islands, 1958. CSIRO Division of Wildlife Research Tech. Pap. No. 6.



Fig. 1. The Lowendal Islands and their location

TABLE 1: BIRDS RECORDED FROM LOWENDAL ISLANDS BY SERVENTY AND MARSHALL IN 1958

=====	
Wedge-tailed shearwater	<i>Puffinus pacificus</i> (Gmelin)
Pied cormorant	<i>Phalacrocorax varius</i> (Gmelin)
Reef heron	<i>Egretta sacra</i> (Gmelin)
Pied goose	<i>Anseranas semipalmata</i> (Latham)
Osprey	<i>Pandion haliaetus</i> (L.)
Kestrel	<i>Falco cenchroides</i> (Vigors and Horsfield)
Pied oyster-catcher	<i>Haematopus ostralegus</i> (L.)
Sooty oyster-catcher	<i>Haematopus fuliginosus</i> (Gould)
Red-capped dotterel	<i>Charadrius alexandrinus</i> (L.)
Caspian tern	<i>Hydroprogne caspia</i> (Pallas)
Silver Gull	<i>Larus novae-hollandiae</i> (Stephens)
Bar-shouldered dove	<i>Geopelia humeralis</i> (Temminck)
Welcome swallow	<i>Hirundo neoxena</i> (Gould)
Australian pipit	<i>Anthus novae-seelandiae</i> (Gmelin)
Yellow silvereye	<i>Zosterops lutea</i> (Gould)
Singing honeyeater	<i>Meliphaga virescens</i> (Vieillot)
White-breasted wood-swallow	<i>Artamus leucorhynchus</i> (L.)

TABLE 2: PLANT SPECIES RECORDED FROM LOWENDAL ISLANDS IN SEPTEMBER 1980

SPECIES	ISLAND:	A	B	C	D	E	F	G	H	J	K	L	M
<i>Abutilon exonemum</i> F. Muell.		*	*	*			*						*
<i>Abutilon leucopetalum</i> F. Muell.				*									
<i>Acanthocarpus preissii</i> Lehm.			*										
<i>Amaranthus viridis</i> L.		*	*	*	*		*	*	*	*	*	*	*
<i>Atriplex isatidea</i> Moq.		*	*			*			*				*
<i>Atriplex semilunaris</i> Aellen		*										*	*
<i>Avicennia marina</i> (Forst.) Vierh.		*	*	*									
<i>Boerhavia mutabilis</i> R.Br.		*	*	*									*
<i>Boerhavia repanda</i> Willd.		*	*	*	*		*				*		
<i>Calandrinia balonensis</i> Lindl.													*
<i>Canavalia rosea</i> (Sw.) DC.				*	*	*							*
<i>Capparis spinosa</i> L.		*	*	*				*		*		*	*
<i>Capparis</i> sp., RB 7155			*										*
<i>Cassytha filiformis</i> L.		*	*										*
<i>Chamaesyce</i> sp. 1		*											*
<i>Chamaesyce</i> sp. 2		*	*	*	*						*		
<i>Chamaesyce australis</i> (Boiss.) Hassall			*										*
<i>Chamaesyce myrtoides</i> (Boiss.) Hassall		*	*						*				
<i>Chrysopogon fallax</i> S.T. Blake													*
<i>Commelina ensifolia</i> Benth.			*										
<i>Corchorus parviflorus</i> (Benth.) Domin.			*										
<i>Dactyloctenium radulans</i> (R.Br.) Beauv.												*	*
<i>Dicladantha forrestii</i> F. Muell.			*										
<i>Digitaria</i> sp., RB 7040													*
<i>Dysphania plantaginella</i> R.Br.													*
<i>Enchylaena tomentosa</i> R.Br.			*	*									*
<i>Eragrostis basedowii</i> Jed.			*	*									
<i>Eulalia fulva</i> (R.Br.) Kuntze			*										
<i>Euphorbia tannensis</i> Spreng.		*	*	*	*								*
<i>Ficus platypoda</i> (Miq.) A.Cunn. ex Miq.			*	*									*
<i>Flaveria australasica</i> Hook.		*	*										
<i>Gomphrena conferta</i> Benth.			*	*									*
<i>Goodenia microptera</i> F. Muell.			*	*									
<i>Indigofera trita</i> L.			*	*									*
<i>Ipomoea pescaprae</i> (L.) R.Br.			*										
<i>Launaea sarmentosa</i> (Willd.) Alston		*	*						*				*
<i>Lawrencina</i> sp., RB 7137		*	*	*									
<i>Lepidium leptopetalum</i> F. Muell.			*										
<i>Melhania incana</i> Heyne		*	*	*								*	*
<i>Myoporum acuminatum</i> R.Br.			*	*	*		*			*			
<i>Neobassia astrocarpa</i> (F. Muell.) AJ Scott			*	*			*	*	*	*		*	*
<i>Nicotiana occidentalis</i> Wheeler		*	*	*								*	*
<i>Panicum australiense</i> Domin.		*											
<i>Pittosporum phillyraeoides</i> D.C.			*	*									
<i>Plumbago zeylanica</i> L.		*											
<i>Portulaca intraterranea</i> J.M. Black		*	*	*			*		*	*	*	*	*

TABLE 2: PLANT SPECIES RECORDED FROM LOWENDAL ISLANDS IN SEPTEMBER 1980

[illegible]

NOTES ON A BRIEF VISIT TO SERINGATAPAM ATOLL
NORTH WEST SHELF, AUSTRALIA

by B.R. Wilson

INTRODUCTION

In October 1978, the author joined the Soviet Research Vessel 'Professor Bogorov' during a cruise in Northern Australian waters. Three working days were spent at Seringapatam Atoll on the North West Shelf. This reef is of great interest to students of Australian coral reefs and marine biogeography because of its geographic position and because it is one of the very few atolls in Australian waters. There are no published records of its biology and little on its geology. Therefore, although there was too little time for detailed studies, it seems appropriate to place on record observations made on the structure of the reef and its fauna.

The expedition was one of a series conducted by the Pacific Institute of Bio-organic Chemistry, Far-East Science Centre, Vladivostok. The basic objective of the expedition was to conduct comparative chemical and biochemical studies of marine invertebrates and algae inhabiting coral reefs with particular reference to some low molecular compounds and biopolymers which possess anti-tumoral and anti-fungal activities.

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Atoll Res. Bull. No. 292: 83-100, 1985.

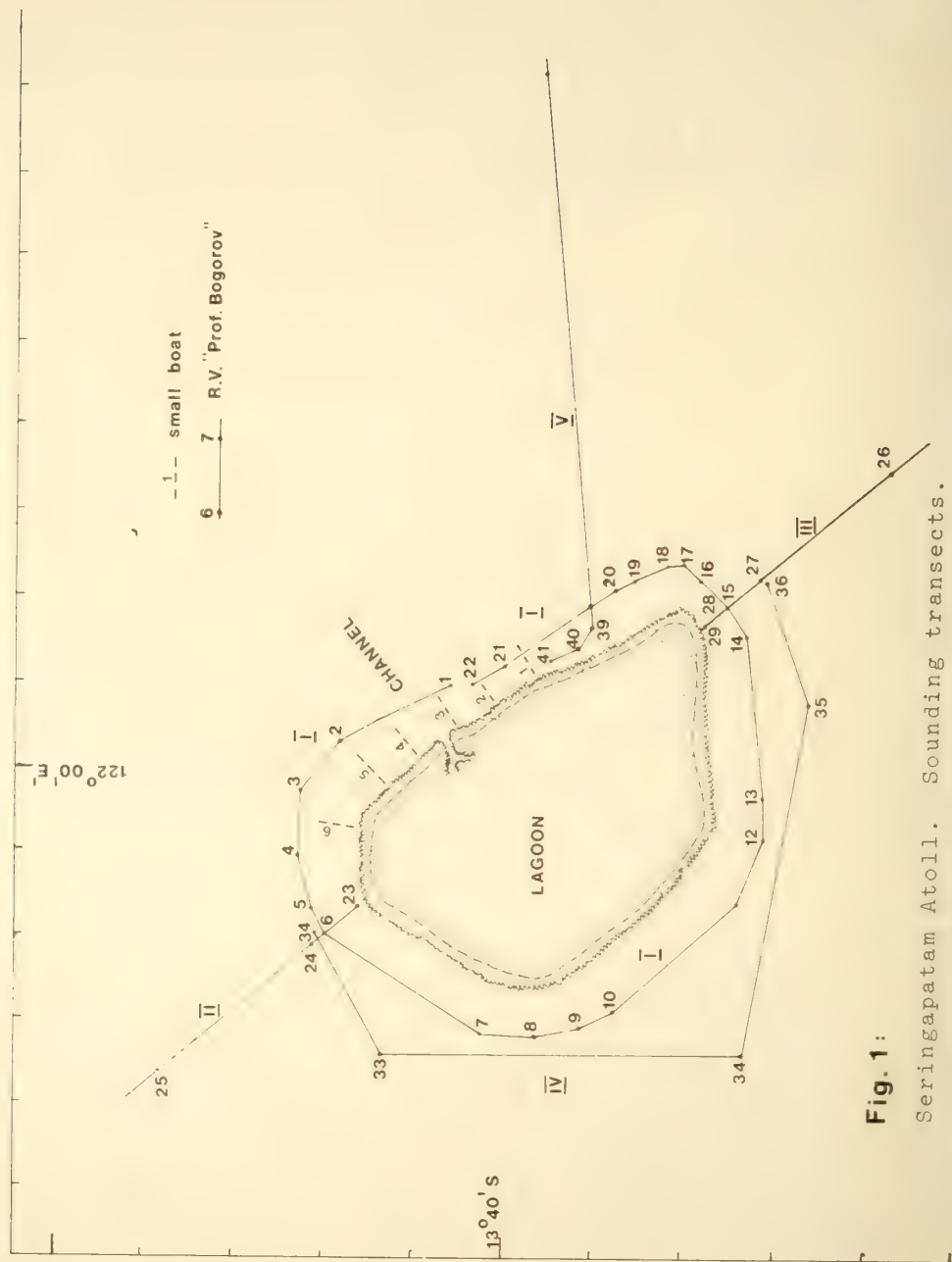


Fig. 1:
Seringapatam Atoll. Sounding transects.

REEF STRUCTURE AND FORM

Position. On the Australian hydrographic chart (1047) Seringapatam Atoll is shown with its centre at $13^{\circ} 40'S$, $122^{\circ} 5'E$. However, the Master of the 'Professor Bogorov', by use of 'Sputnik' fixes, advised that the approx. centre of the lagoon has the co-ordinates $121^{\circ} 59' 35"E$, $13^{\circ} 40' 35"S$.

Shape and Dimensions. Seringapatam Reef is an atoll possessing the habitats typical of Indo-West Pacific inundated atolls. The atoll is roughly trapezoidal with the longest (NE) side being almost straight and bearing about 140° . Its length is approximately 4.5 nautical miles (NW-SE) and its maximum width approximately 3 nautical miles (Fig. 1). The peripheral reef, which varies from 300-500m wide, encloses a broad and deep lagoon.

Relief and Geology. At high tide no emergent structures are visible but at mid and low tide the central part of the annular limestone reef emerges. The highest zone or reef crest is located about 100m behind the outer reef edge and behind that the back-reef varies from about 200 to 300m wide.

Reef flat. Around the entire perimeter of the atoll on the reef crest there is a well developed 'boulder zone' which provides conspicuous irregular relief to the reef when seen from a distance at mid or low tide. Most of the boulders are free-lying blocks of reef limestones; relatively few are coral slabs. In addition to the 'loose' boulders there are many 'attached' erosional relics, or stacks, which are part of the limestone substrate, the highest being about 2m tall (Plate 1). Many of them are mushroom-shaped, have a dense calcrete capping and are deeply undercut by biological and physical erosive forces (Plate 2). Burrowing barnacles (*Lithotrya valentiana*) are the principal biological erosive agent. Those which have been completely undercut have toppled to become reef crest boulders.

The reef limestone itself is fossiliferous, containing abundant fossil corals and some molluscs. It is assumed to be of Pleistocene age.

Large sand cays exposed at low tide were observed in the back-reef zone at the NW and NE corners. There may be others at the southern end although none were visible when the ship passed around that end of the atoll at low to mid tide.

Channels. A shallow, bent channel was located on the NE side at about $122^{\circ} 0' 15''\text{E}$, $13^{\circ} 40''\text{S}$ (Fig. 1). It can be entered only by small vessels drawing less than about 2.5m and only at high to mid tide. At low tide there is a torrent of water pouring out of the lagoon making extremely turbulent and hazardous conditions. The channel is about 80m wide at its seaward entrance and narrows and divides as it enters the lagoon where there is a dangerous central patch reef which is very difficult to see in the late afternoon due to the angle of the sun. The deepest and safest arm of the inner channel turns NW.

There may be other similar channels into the lagoon, perhaps at the southern side, but none could be located.

Reef Front (= fore-reef). This was examined at a number of locations along the NE side. There the intertidal part of the reef-flat (i.e. seaward of the reef crest to the reef-edge) has a width of about 100m. There is no raised rim at the reef-edge and no prominent spurs and grooves or drainage gutters; the reef-flat slopes gently, or with a series of little terraces up to 10cm high, to the reef-edge (Plate 3). Periodic broad, shallow, depressed zones carry the out-flowing water off the reef-flat at low tide. The reef-edge itself is very irregular and indistinct. There is little living coral or crustose coralline algae on the reef-front which has a close-cropped cover of leafy brown algae.

From the intertidal reef-edge there is a broad reef-front slope progressing seaward for a distance of 100-150m apparently around the entire perimeter of the atoll. On the side of the atoll which was examined (NE), the upper part of this zone is gently sloped with an average angle of about 5° . It is characterized by high sub-tidal spurs or ridges roughly normal to the reef-edge and bearing moderate growths of living scleractinian corals, alternating with deep

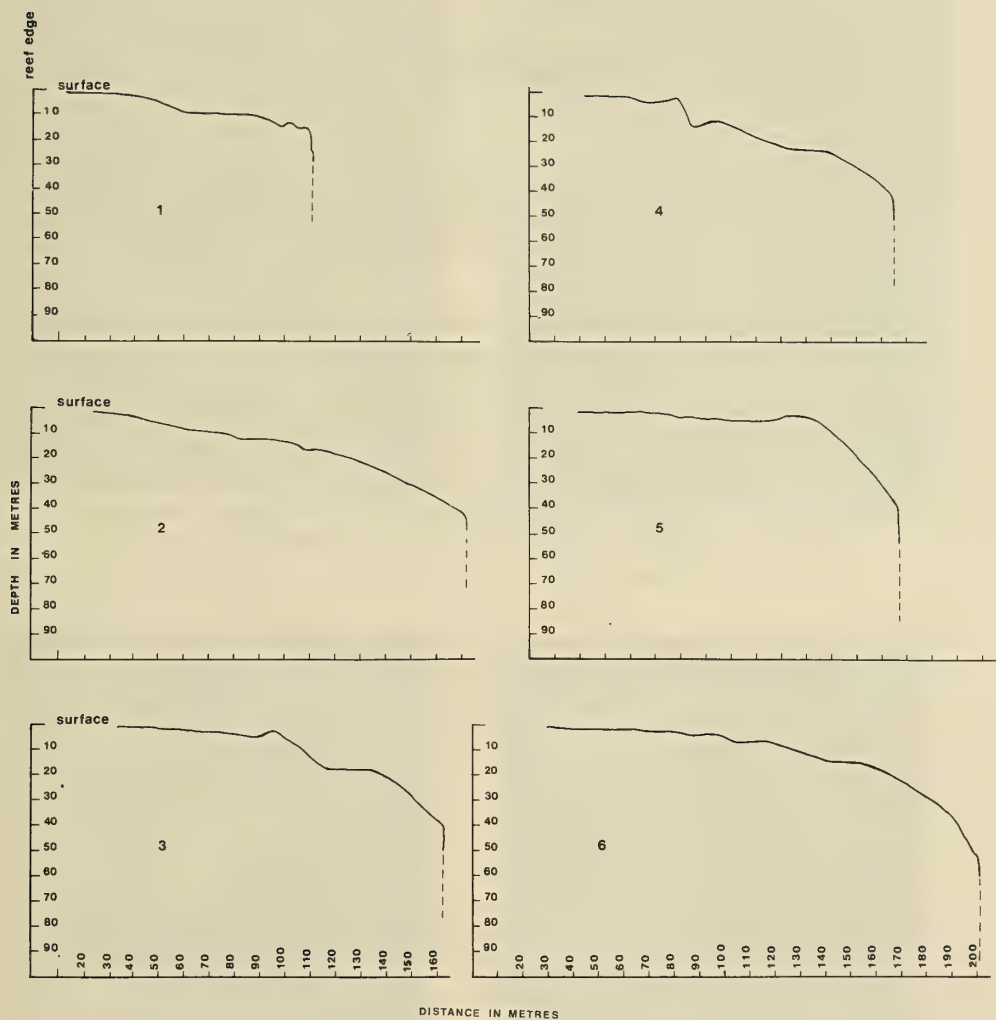


Fig. 2

Small boat sounding transects 1 to 6 across the reef-front slope normal to the edge along the NE side of Seringapatam Atoll.

PLATE CAPTIONS

- Plate 1: Residual reefal limestone stack on the reef-crest, NE side of Seringapatam Atoll. Note also the numerous free-lying boulders.
- Plate 2: Residual reefal limestone stack with lithified crust on the reef-crest, NE side of Seringapatam Atoll. Note extensive burrowing by barnacles on the sides.
- Plate 3: The weakly terraced reef-edge at the NE side of Seringapatam Atoll at low-tide.
- Plate 4: Valeriy Kiselev sampling alcyonarians on the vertical wall, NE side of Seringapatam Atoll; 55m.



Plate 1

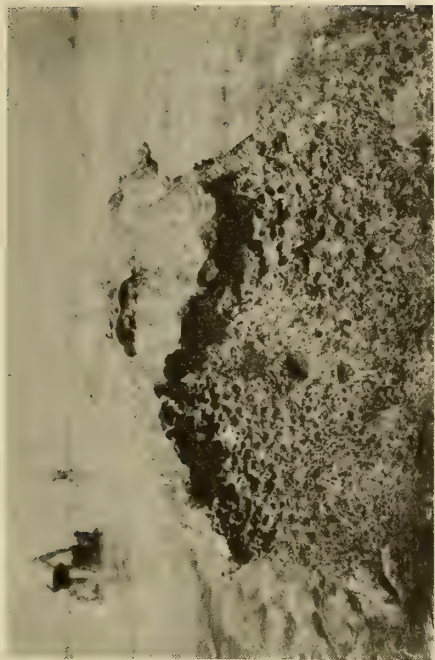


Plate 2

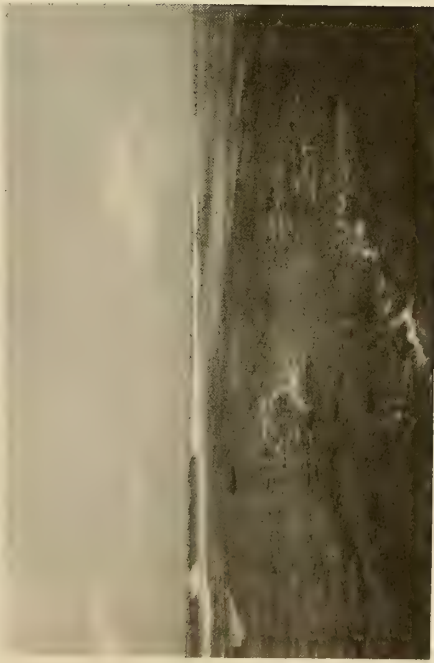


Plate 3



Plate 4

grooves or gutters which have coarse sand and coral boulders and rubble on their beds. The sides of the spurs are deeply undercut and cavernous. The spur and groove system terminates at a depth of about 12-15m. Below this the slope increases to about 15° . Here coral rubble and soft corals predominate but there are some living scleractinians. The reef-front slope terminates abruptly at the edge of a vertical 'drop-off' at 30-40m. Deep dives down the drop-off wall were made at 4 localities in the vicinity of the channel (between stations 5 and 3) to depths of 60 to 80m. Narrow ledges no more than 1m or so wide are the only horizontal features of the wall as far down as 75m. At that depth a steep rubble slope (ca. 25°) was observed, but this too was only 10-12m wide and below that was another vertical wall which continued out of sight. There is little scleractinian coral growth on the vertical rock face, but numerous soft corals and tree-like gorgonians (Plate 4).

A series of small-boat sounding transects normal to the reef-edge along the NE side confirmed the existence of the vertical drop along the whole length of that side (Fig. 2). The traces ended abruptly at the drop-off edge because the depth at the foot of the vertical wall exceeded the maximum range of the sounder used (110m).

No equivalent deep dives or small-boat sounding transects were made on the NW, SW and S sides of the atoll and it was not determined whether there is a vertical rock wall there also. However, 'Bogorov' echo-sounding traverses as close as possible, both around and normal to the reef (Figs. 1 & 3) show that there is at least an extremely steep if not vertical 'slope' around the entire perimeter of the atoll down to about 200m. Below that there is a steep slope of about 35° to the sea floor which is reached at about 500m at the SE end and 750m at the NW end (Fig. 3).

Back-Reef. Behind the reef crest there is a wide back-reef zone, rich in living corals in the outer part and sloping very gently back to a sandy inner part. At its sandy inner edge, at a depth of about 5m, the back-reef slope begins, angling abruptly (ca. $20-30^{\circ}$) down to the bottom of the lagoon. On this steep slope

and on the sandy inner back-reef there are extensive dense patches of staghorn *Acropora* corals.

Lagoon. A small boat sounding traverse was made down the centre of the northern part of the lagoon. The maximum depth measured was 27m. The bottom is very irregular with numerous coral patch reefs, mounds and pinnacles but these rarely rise closer than 2m to the surface. (Thus, once entered the lagoon is freely navigable by small boats.)

At a diving station near the centre of the lagoon the bottom sediment was found to consist of thick, white, calcareous silt. Bottom visibility when undisturbed was only 3-4m. Corals were diverse in patches; staghorn *Acropora* species were the most abundant but many foliose corals such as *Pachyseries*, *Echinophyllia*, *Merulina* and massives like *Lobophyllia* were also common.

DISCUSSION

Teichart & Fairbridge (1948), Jones (1973), Hinz et al (1978) and others have discussed the geological history of the North West Shelf and Sahul Shelf region. The outer part of the shelf is believed to have been subjected to substantial subsidence since the Mesozoic. Seringapatam, its neighbour Scott Reef and the Rowley Shoals further south, rise from the sea floor of the depressed continental slope at depths of 500 to 800m. Seringapatam and Scott lay on the crests of anticlinal trends. Below Scott Reef there is a thickness of more than 2000m of Tertiary and Quaternary reefal limestone (Jones, 1973). Faulting is common along the shelf margin in this region; the fault direction is usually NW, ie normal to the margin (Jones, 1973).

Thus, and taking account of its extremely steep and rather straight-sided, trapezoidal form, it seems reasonable to interpret Seringapatam as a coral reef structure of considerable antiquity, built originally (early Tertiary?) upon an upthrust block in the faulted basement. The strikingly straight NE side, for example, lies in the regional fault direction and implies that the shape and character of this atoll are structurally controlled. Continuing regional subsidence and rapid reef growth since the early Tertiary has resulted in the present flat-topped, tower-like structure. The

vertical sides in the upper 200m or so are probably a result of coral growth and terrestrial erosion in successive Pleistocene eustatic stages.

The undercut stacks of the reef-flat boulder zone are interpreted as erosional relics of an earlier reef-flat which stood about 2m higher than the present one. The rate of erosion is very rapid and the age of the higher reef-flat was probably Holocene.

MARINE FAUNA

Several hours were spent during the afternoons of October 14 and 15 on the reef-flat at low tide at a location on the NE side of the atoll about 0.5km north of the channel. Some hand collecting was done there. Collections were also made by snorkel and scuba diving in the lagoon and along the reef-front slope on the NE side.

Voucher specimens of the samples from which the ship's biochemists took extracts for analysis were lodged at the W.A. Museum for future reference. Other specimens of echinoderms, molluscs and some scleractinian corals, representative of the common elements of the fauna, were also collected and lodged at the W.A. Museum.

Although these collections were far from exhaustive they seem sufficient to characterize the invertebrate fauna. Figure 4 shows diagrammatically the reef-flat habitats sampled.

Habitat Zones:

1. The platform surface, crevices and shallow pools of the outer reef-flat.
2. Under coral and reef-rock slabs of the reef crest.
3. On high rocks and stacks of the high intertidal zone on the reef crest.

4. Sand and rubble substrates of the back-reef shallows.
5. Under coral and reef-rock slabs of the back-reef shallows.

Tables 1 and 2 list the common macro-molluscs and echinoderms taken.

CORALS

Although no extensive collection of corals was made during this expedition the variety observed was great in the lagoon where many ramose, foliose, massive and encrusting forms occurred. On the other hand, growth of hard corals on the reef-front slope seemed less luxuriant than on many near-shore reefs further south on the Western Australian coast.

Soft corals were a conspicuous feature of the benthic fauna, especially on the lower parts of the reef-front slope on the NE side of the atoll where they outnumbered scleractinians. In that situation the alcionacean genera *Nephtya*, *Alcionia*, and *Alcionaria* were especially abundant, as were the gorgonaceans *Plexaura* and *Gorgonia*. These animals were sampled extensively by the biochemists.

ECHINODERMS

A representative series of the common echinoids and asteroides was retained (Table 2). The material identified indicates that the echinoderm fauna is typical of the Central Indo-West Pacific region. Many holothurians were collected for biochemical analysis but not all the specimens were kept for subsequent identification. No crinoids and only a few ophiuroids were collected.

MOLLUSCS

The macro-molluscs of the reef-flat form a community typical of oceanic atolls and reefs of the Central Indo-West Pacific region with browsing and predatory prosobranchs being most conspicuous. The fauna is

different in several respects to the analogous reefs on the coastal islands of the Western Australian coast.

The common *Modiolus* is *M. auriculatus*, a very widespread intertidal mussel found on clear-water, oceanic reefs. On the turbid-water coastal reefs north of North West Cape, this species is absent and instead one finds there *M. nipponicus* Oyama, 1950.

On the mainland and coastal reefs, coral rocks and boulders of the reef-flat are heavily bored by *Lithophaga teres*, *L. obesa*, *L. nasuta* and *L. malaccana*. At Seringapatam species of *Lithophaga* were not seen and instead the coral boulders of the reef-crest (Zone 3) were heavily bored by the cirripede *Lithotrya valentiana*. There were no oysters on the high intertidal rocks and stacks; the only molluscs collected there were *Patella flexuosa*, *Nerita* sp., and *Thais armigera*.

Cerithium nodulosum, *Cypraea histrio*, *C. depressa* and *Lambis chiagra* are all conspicuous gastropods on the Seringapatam reef-flat (Zones 1 and 2) but these are absent or rare on the northern coastal reefs where the water is more turbid. (*Lambis chiagra* and *Modiolus auriculatus* are found on the fringing reef south of North West Cape where the water is clear.)

Faunal differences of this kind are interpreted as ecological, the fauna of Seringapatam showing the characteristics of an isolated oceanic atoll not subjected to turbid coastal water.

Another noteworthy feature of the fauna is the presence of the Pacific thaid *Nassa sarta*. On the mainland and coastal reefs, including those south of North West Cape, the Indian Ocean species *Nassa francolina* Bruguière occurs but not *N. sarta*. Also, on the coastal reefs, the Indian Ocean species *Drupina lobata* Blainville occurs together with the Pacific *D. grossularia*, while at Seringapatam only the latter is found. These observations suggest that the intertidal fauna of Seringapatam lacks the peculiarly Indian Ocean elements in favour of their Pacific analogues.

DISCUSSION & SUMMARY

The intertidal invertebrate fauna of Seringapatam is typical of Indo-West Pacific oceanic atolls and seems to have a Pacific rather than Indian Ocean flavour. This is not inconsistent with the location and the north-easterly ocean currents.

There is a very diverse scleractinean coral fauna although soft-corals dominate the reef-front slope, at least along the NE side.

The reef-flat molluscan fauna is dominated by browsing and predatory prosobranchs. Suspensory-feeders are uncommon.

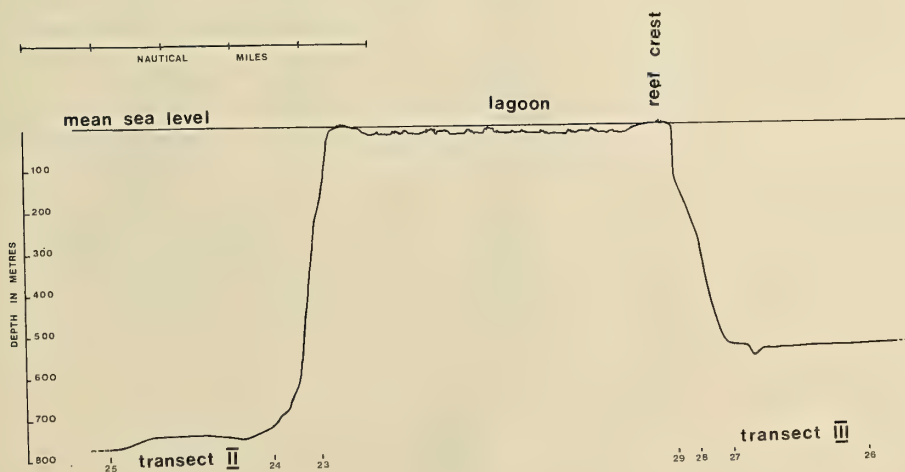


Fig. 3 : Diagrammatic section through Seringapatam Atoll along the NW-SE axis, derived from sounding transects II and III by the R.V. 'Professor Bogorov' and observations on the reef.

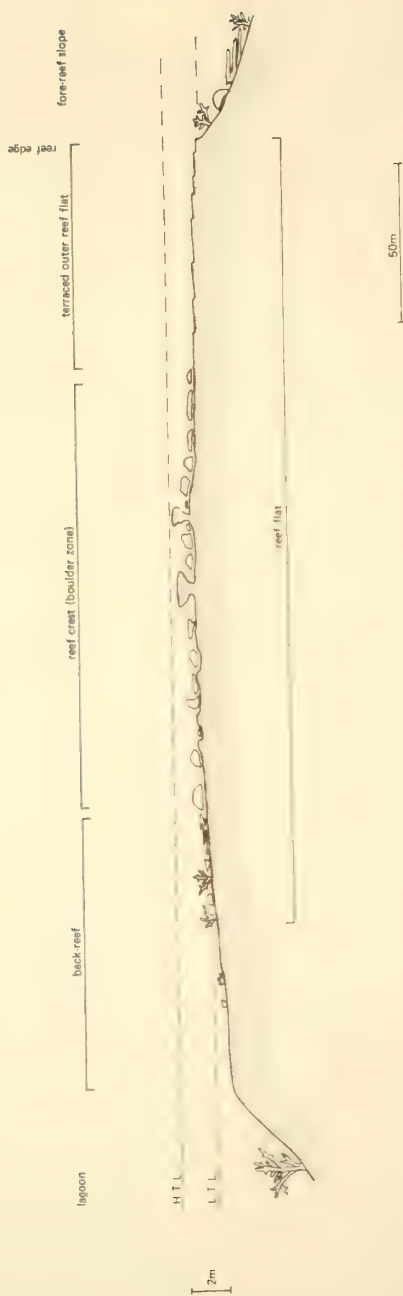


Fig. 4 :

Diagrammatic section across the reef of Seringapatam Atoll in the vicinity of small boat transect 5 (see Fig. 1), showing habitat zones described in the text.

TABLE 1 Common molluscs of the reef flat in the vicinity of small-boat transect 5. See Figure 4 and text for explanation of zones.

<u>MOLLUSCS</u>	<u>ZONES</u>				
	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>
<i>Modiolus auriculatus</i> Krauss, 1848	x				
<i>Tridacna maxima</i> Røding, 1798	x				
<i>Tridacna squamosa</i> Lamarck, 1819				x	
<i>Hippopus hippopus</i> (Linnaeus, 1758)				x	
<i>Fragum fragum</i> (Linnaeus, 1758)				x	
<i>Marmarostoma chrysomus</i> (Linnaeus, 1758)		x			x
<i>Trochus maculatus</i> Linnaeus, 1758		x			
<i>Trochus pyramis</i> Born, 1778	x	x			x
<i>Patella flexuosa</i> Quoy & Gaimard, 1834			x		
<i>Nerita</i> sp.			x		
<i>Cerithium nodulosum</i> Bruguiere, 1792	x			x	
<i>Cerithium echinatum</i> Lamarck, 1822	x				
<i>Rhinoclavis</i> sp.	x				
<i>Strombus lentiginosa</i> Linnaeus, 1758				x	
<i>Lambis chiagra</i> Linnaeus, 1758	x				
<i>Cypraea caputserpentis</i> Linnaeus, 1758	x	x			
<i>Cypraea histrio</i> Gmelin, 1791		x			
<i>Cypraea depressa</i> Gray, 1824		x			
<i>Cypraea lynx</i> Linnaeus, 1758		x			
<i>Cypraea isabella</i> Linnaeus, 1758		x			
<i>Cypraea tigris</i> Linnaeus, 1758		x			
<i>Cypraea moneta</i> Linnaeus, 1758					x
<i>Bursa bufonia</i> Gmelin, 1791		x			
<i>Bursa cruentata</i> Sowerby, 1835		x			
<i>Nassa sarta</i> Bruguiere, 1789		x			
<i>Peristernia nassatula</i> Lamarck, 1822		x			
<i>Vasum ceramicum</i> Linnaeus, 1758	x				
<i>Vasum turbinellum</i> Linnaeus, 1758	x				
<i>Latirolagena smaragdula</i> Linnaeus, 1758	x				
<i>Thais armigera</i> Link, 1807			x		
<i>Thais</i> sp.			x		
<i>Drupina grossularia</i> Røding, 1798	x				x
<i>Drupina ricinus</i> Linnaeus, 1758	x				
<i>Chicoreus brunneus</i> (Link, 1807)	x				
<i>Conus lividus</i> Hwass, 1792	x				
<i>Conus flavidus</i> Lamarck, 1810	x				
<i>Conus miles</i> Linnaeus, 1758	x				x
<i>Conus rattus</i> Hwass, 1792	x				
<i>Conus imperialis</i> Linnaeus, 1758	x				
<i>Conus marmoreus</i> Linnaeus, 1758	x				
<i>Conus coronatus</i> Gmelin, 1791	x				
<i>Conus sponsalis</i> Hwass, 1792	x				

TABLE 2 Common echinoderms of the reef flat in the vicinity of small-boat transect 5. See Figure 4 and text for explanation of zones.

	<u>ZONES</u>				
	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>
<u>ECHINODERMS</u>					
<i>Parasalenia gratiosa</i> A. Agassiz, 1863; burrowing in the outer surface of <i>Tridacna maxima</i>					x
<i>Echinometra mathaei</i> (de Blainville, 1825); burrowing in hard reef surface					x
<i>Echinothrix diadema</i> (Linnaeus, 1758); pools					x
<i>Tripneustes gratilla</i> (Linnaeus, 1758); pools					x
<i>Eucidaris metularia</i> (Lamarck, 1816)					x
<i>Echinoneus cyclostomus</i> Leske, 1778; buried in sand under stones					x
<i>Culcita novaeguinae</i> Muller & Troschel, 1842; pools					x
<i>Linkia laevigata</i> (Linnaeus, 1758); pools and reef surface					x
<i>Linkia multifora</i> (Lamarck, 1816)					x
<i>Ophidaster granifera</i> Lutken, 1872					x
<i>Asterina cepheus</i> (Muller & Troschell, 1842)					x
<i>Astereopsis carinifera</i> (Lamarck, 1816)					x
<i>Nardoa tuberculata</i> Gray, 1840					x
<i>Lehinaster luzonica</i> (Gray, 1840)					x
<i>Stichopus chloronotus</i> Brandt, 1835					x
<i>Thelonota ananus</i> (Jaegar, 1833)					x
<i>Bohadschia argus</i> Jaegar, 1833					x
<i>Ophiarthrum pictum</i> Muller & Troschell, 1842					x
<i>Ophiocoma deoderleini</i> de Loric, 1899					x
<i>Ophiarachna incrassata</i> (Lamarck, 1816)					x

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While aboard the 'Professor Bogorov' I was treated with extraordinary hospitality and given much help in pursuing my interests. I sincerely thank Captain Gennady Nozdrin, and the Expedition Chief, Dr Valeriy Rasskazov for their hospitality and good fellowship and all those members of the crew who made the expedition such a memorable one for me. In particular, I wish to acknowledge the friendship and assistance of my diving 'buddy', the late Valeriy Kiselev who drowned recently in the North Pacific.

I am especially grateful to Mrs L.M. Marsh of the Western Australian Museum and Dr F. Rowe of the Australian Museum for identifying the echinodermus.

REFERENCES

- Hinz, K., Beiersdorf, H., Exon, N.F., Roeser, H.M., Staff, H.M.J., and Stackelberg, U. von (1978). Geoscientific investigations from the Scott Plateau off north-west Australia to the Java Trench. B.M.R. J. Aust. Geol. & Geophys. 3: 319-340.
- Jones, H.A. (1978). Marine Geology of the North-West Australian Continental Shelf. B.M.R. Bull. 136: 1-102, 2 maps.
- Teichert, C. and Fairbridge, R.W. (1948). Some Coral Reefs of the Sahul Shelf. Geogr. Rev. 38: 222-249.

SEA SNAKES COLLECTED AT CHESTERFIELD REEFS, CORAL SEA

by Sherman A. Minton and William W. Dunson¹

INTRODUCTION

This report describes a collection of sea snakes made at the Chesterfield Reefs June 19-25, 1981. We know of no previous collection of sea snakes from this locality. The Chesterfields are a group of reefs and sand cays located in the southern part of the Coral Sea about 945 km ENE of Rockhampton, Queensland and about 630 km almost due west of the northern tip of New Caledonia (Fig. 1). Troughs with depths of 1000-3000 m separate them from New Caledonia and the Great Barrier Reef complex. Loop Islet at the southern tip of the group (Fig. 2) lies at 19° 57' south and 158° 28' east.

METHODS

Most snakes were captured in nets while snorkling or scuba diving at depths of 20 m or less. Underwater visibility was generally good, and water temperatures 22-25°C. A few snakes were netted from small boats or from the R/V Acheron or were found stranded on sand cays. A total of 79 snakes was collected and 34 preserved. These have been deposited in the Field Museum of Natural History, Chicago, and the Australian Museum, Sydney. Six species were identified in the material collected.

RESULTS

Acalptophis peronii (4 collected; 2 preserved). All specimens were taken over relatively flat, open areas of sand at depths of about 10-15 m. The smallest had a total length of 45 cm, the largest measured about 85 cm.

Aipysurus duboisii (2 collected and preserved). One specimen was collected in a narrow coral passage at a depth of 14 m; the other was found stranded and dead on Anchorage Islet. Total lengths were 83 and 74 cm.

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Aipysurus laevis (2 collected; 1 preserved). One taken on the side of a bommie at a depth of about 6 m; the other over open sand at about 15 m. Both were small adults about 1 m in total length.

Emydocephalus annulatus (15 collected; 7 preserved). Five were found over open sand, the others in coral passages or around bommies. Depths varied from 3 to 15 m. One large snake was probing crevices in a bommie while two small fish seemed to be harassing it by biting at its neck. It reacted by shaking them off occasionally. After about 10 minutes the snake glided into deeper water and continued to explore coral rubble; the fish did not follow. Another snake had its head and forebody in a hole in the sand. A courting pair of snakes were observed June 21. Three juveniles 31-34 cm in total length were taken. The smallest of these was lying dead on the bottom. Five of 6 preserved adults were uniformly black; one large female showed numerous cream-colored scales irregularly scattered. Two adults of the ringed pattern morph were seen.

Hydrophis sp. (40 collected; 20 preserved). This small-headed sea snake was plentiful off Loop Islet in an area of flat, open sand lightly covered with filamentous algae at a depth of 7-11 m. The snakes were usually seen lying on the bottom often with the head and forebody buried in sand or were swimming slowly a few centimeters above the bottom. Five were collected by dip-netting from the ship while anchored off Passage Islet at night and others were seen in the illuminated zone but escaped. Several of the snakes were juveniles 40-50 cm long. No food was disgorged by newly captured snakes, but the digestive tract of one adult contained a brown, pasty, homogeneous material. These snakes are similar to specimens collected at reefs of the Sahul Shelf and referred to Hydrophis melanocephalus (Cogger, 1975). They also fit the description of H. melanocephalus from Fiji (Guinea, 1981) and probably are identical with the species taken at Saumarez Reef and identified as Microcephalophis gracilis (Heatwole, 1975). However, they appear to differ significantly from both melanocephalus and gracilis from Asian waters and probably represent an undescribed taxon whose status is currently under investigation.

Pelamis platurus (11 collected; 2 preserved). Eight of these snakes were collected June 23 in a slick on the lagoonal side of the inlet north of Passage Islet. The others were found stranded on Loop and Anchorage Islets. One was seen at night near the ship. Desiccated remains of 5 other Pelamis were found on beaches. One had been incorporated into the nest of a booby. Four of the snakes collected were juveniles about 35-40 cm in total length. Two of the others were very dark, large individuals, one female having a total length 98 cm.

We presume all the species are residents of the Chesterfields rather than strays, for multiple individuals of all were collected. Collection of juveniles of 4 species suggests local breeding.

DISCUSSION

Table 1 summarizes information of sea snake distribution along the Queensland Coast, the southern part of the Great Barrier Reef, the Chesterfield Reefs, New Caledonia and the Loyalty Islands, and Fiji. Species diversity is greatest along the Queensland coast probably because species with preference for turbid water and a muddy bottom such as Aipysurus eydouxi, Lapemis hardwickii, Enhydrina schistosa, and Hydrophis elegans find favorable habitat here but not on the Great Barrier Reef or eastward. The first three species have extensive ranges indicating good powers of dispersal. Mud and turbidity may largely exclude Emydocephalus annulatus, a snake of clear water and coral reefs, from the coastal zone. Aipysurus laevis and A. duboisii are characteristic coral reef species that also are locally plentiful along the Queensland coast. Pelamis platurus is not known to breed along the Queensland coast, although beach-washed individuals are encountered regularly. It is uncommon on the Great Barrier Reef but appears to have a well-established population in the Chesterfields. Laticauda colubrina and L. laticaudata are reported to be common in waters around New Caledonia and the Loyalty Islands and also occur at Fiji. They are unknown from the Great Barrier Reef and recorded from the eastern coast of Australia only very rarely. They appear to have reached New Caledonia from the northwest by dispersal along the New Hebrides Ridge. Availability of suitable daytime resting and seasonal nesting areas may be vital factors influencing distribution of these oviparous sea snakes. Astrotia stokesii and Hydrophis ornatus are wide-ranging and presumably eurytopic species that may eventually be found in the Chesterfields.

ACKNOWLEDGMENTS

Supported by NSF grant PCM 79-18393 to W.A.D. We are grateful to the University of New England, Armidale, N.S.W., for serving as the official sponsor of the expedition. Dr. Harold Heatwole's assistance, advice, and enthusiastic participation in the expedition contributed greatly to its success. We also appreciate the help of Glen Burns, Glenn Stokes, and David Berman in catching snakes.

LITERATURE CITED

- Dunson, W.A. 1975. Sea snakes of tropical Queensland between 18° and 20° south latitude. In W.A. Dunson (ed.) The Biology of Sea Snakes, Baltimore, University Park Press, pp. 151-162.
- Cogger, H.G. 1975. Sea snakes of Australia and New Guinea. In Dunson, op. cit., pp. 114-115.
- Forne, F. 1888. Sur un cas de mort par morsure du serpent de mer. J. Offic. N. Caledonie et Depend., no. 1520, pp. 335-341 (not seen)
- Gail, R. and Rageau, J. 1958. Introduction a l'etude des serpents marins en Nouvelle-Caledonia. Bull. Soc. Path. Exot. 51: 448-459.

- Guinea, M.L. 1981. The sea snakes of Fiji. Fourth Internat. Coral Reef Symp.
- Halstead, B.W. 1970. Poisonous and Venomous Marine Animals of the World, Washington, D.C., Government Printing Office, vol. III, pl. xxxii.
- Heatwole, H. 1975. Sea snakes found on reefs in the southern Coral Sea (Saumarez, Swains, Cato Island). In Dunson, op. cit., pp. 161-171.
- Limpus, C.J. 1975. Coastal sea snakes of subtropical Queensland waters (23° to 28° south latitude). In Dunson, op. cit., pp. 173-182.
- Roux, J. 1913. Les Reptiles de la Nouvelle-Caledonie et des iles Loyalty. In Sarasin and Roux, Nova Caledonia, Wiesbaden, pp. 76-160 (not seen)
- Smith, M.A. 1926. A Monograph of the Sea Snakes. London, Taylor and Francis.

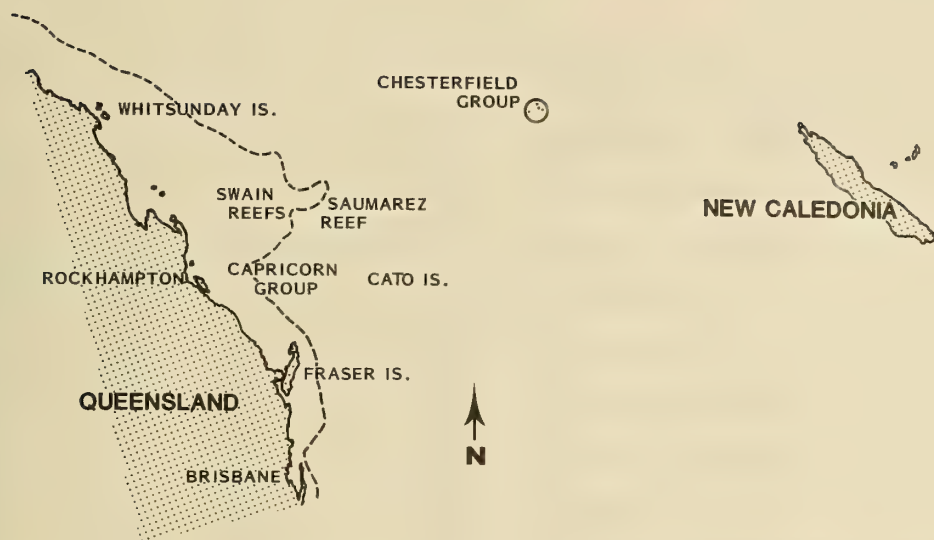


Fig. 1. Location of Chesterfield group with respect to New Caledonia and the Queensland coast. Dashed line marks approximate outer limit of Great Barrier Reef complex.

Fig. 2. Chesterfield Group showing localities mentioned in text. Figures indicate water depths in fathoms.

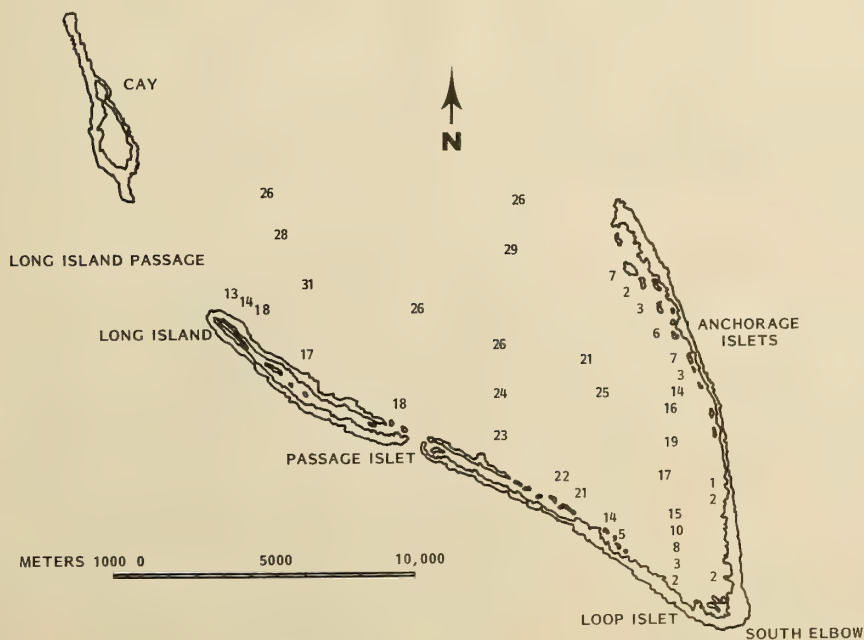


TABLE 1

	<i>Acalyptophis peronii</i>	<i>Aipysurus duboisii</i>	<i>Aipysurus eydouxii</i>	<i>Aipysurus laevis</i>	<i>Astrotia stokesii</i>	<i>Disteira kingii</i>	<i>Disteira major</i>	<i>Emydocephalus annulatus</i>	<i>Enhydryna schistosa</i>	<i>Hydrophis elegans</i>	<i>Hydrophis ornatus</i>	<i>Hydrophis</i> sp. 1*	<i>Hydrophis</i> sp. 2**	<i>Lapemis hardwickii</i>	<i>Pelamis platurus</i>	<i>Laticauda colubrina</i>	<i>Laticauda laticaudata</i>
Queensland Coast: Fraser Is. to Hinchinbrook Is. (Dunson, 1975; Limpus, 1975)	R	X	X	X	X	X	X	R	X	X	X		X	X	U	R	
Southern Barrier Reef, Swains & Saumarez Reefs, Cato Is. (Heatwole, 1975; personal observations)	X	X		X	X	R		X				U					
Osterfield Reefs and Islands	X	X		X				X				X			X		
New Caledonia and Loyalty Is. (Gail and Rageau, 1958; Halstead, 1970; Smith, 1926)	R	X		X			??	X		??	??	??			X	X	X
Fiji Islands (Guinea, 1981)												X			U	X	U

Table 1 (continued)

- X Species at least locally plentiful and presumably breeding in the area.
- R Rare in the area. Records presumably based on stray individuals, not breeding populations.
- U Present but status in the area undetermined.
- * Similar to Sahul Shelf population currently referred to Hydrophis melanocephalus. Probably the species referred to Microcephalophis gracilis by Heatwole (1975).
- ** An apparently undescribed small-headed Hydrophis with ornate pattern. See Dunson (1975) for figure; also Cogger (1975).
- ?* At least two species of Hydrophis-like sea snakes occur in New Caledonia waters. These have been variously identified as Hydrophis caerulescens and Microcephalophis gracilis (Gail and Rageau, 1958), Disteira major (Roux, 1913, cited by Gail and Rageau), and Hydrophis ornatus ocellatus (Forne, 1888, cited by Gail and Rageau).

Table 1. Distribution and abundance of sea snakes in the Chesterfield Islands and nearby areas.

THE UNDERWATER MORPHOLOGY OF PALMERSTON AND SUWARROW ATOLLS

by J. Irwin*

ABSTRACT

Methods used and results of echo sounding surveys of Palmerston and Suvarrow lagoons, Northern Cook Islands, are given in this paper. Notes on the compilation of a bathymetric chart of Palmerston Atoll are given and features of the underwater morphology of each lagoon are described and illustrated.

INTRODUCTION

During September 1981 Palmerston and Suvarrow Atolls in the Northern Cook Islands were surveyed by echo sounder. This work was part of a joint N. Z. Oceanographic Institute and Royal Society of London cruise using the New Zealand Research Vessel R. V. Tangaroa. Sounding coverage was carried out from 5-14 September at Palmerston Atoll but only two days, 20 and 21 September were available for soundings at Suvarrow, allowing only sketch coverage to be made. This note describes the methods and results of the sounding survey and data on water characteristics at the time of survey.

Methods and Equipment:

A 5.5 m aluminium outboard-motor-powered boat and Raytheon survey echo sounder (Model DE 719B) with the transducer mounted overside were used. Additional and comparative echo soundings were made with a Furuno F850 echo sounder. Five stations at Palmerston Atoll and one at Suvarrow Atoll were occupied to collect water samples with National Institute of Oceanography water bottles for salinity readings and water temperatures throughout the water column were recorded using a bathy-thermograph. Data collected was used to correct echo soundings for

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regional variations to the velocity of sound in water. Foxboro tide gauge stations were established at Home and Primrose Islands at Palmerston Atoll and at Anchorage Island and Suvarrow Atoll, all inside the lagoon. Tidal readings from Home Island were used to reduce soundings to a common datum, near low water. This gauge and the gauge at Suvarrow Atoll were referenced to bench marks.

Field plots were made using Atoll outlines from 1974 aerial photography mapped by photogrammetric methods. Original aerial photographs were also available. Sounding traverses were made between known points at constant boat speed. The low relief and large width of the lagoon made navigation difficult. To aid position fixing and shorten traverse lines two large inflatable iridescent red buoys were positioned in an approximate N-S line near the centre of the lagoon. These buoys aided position fixing, shortened traverse lines and provided end points for sounding traverses. Traverse end points were established at atoll islands, identified on aerial photographs, or by compass bearings of positions inside the atoll edge. Compass bearings were used on long traverses to check position along the line. Navigation Chart (B.A. 1147 Suvorov Islands) was used to plot sounding traverses at Suvarrow Atoll. Positions plotted on this chart showed the south west side of the atoll further northwards than depicted, by approximately 0.2 to 0.7 nautical miles, this was confirmed by ships radar from R. V. Tangaroa anchored inside the lagoon. Figure 3 shows Suvarrow atoll from 1974 aerial photography.

Fifty two traverses approximately 400 metres apart gave coverage of Palmerston Atoll for which a bathymetric chart has been prepared for publication (Irwin and Main 1983). Ten echo sounding traverses provided sketch coverage of Suvarrow Atoll.

B.A. Chart 1147 Suvorov Islands shows soundings from surveys of 1900 and 1920; these spot soundings were made before the advent of the echo sounder. The present survey provides continuous sounding traverses depicting bottom configuration, and in the case of Palmerston Island provides new information.

PALMERSTON ATOLL

Situated 500 kilometres NW of Rarotonga, Palmerston Atoll takes the form of a diamond. Groups of islands are situated about the reef concentrated on the N, S, E and W points. Land area is approximately 400 hectares. The lagoon measures 9 km N-S and 6.5 E-W and the exposed reef averages 0.5 km across. Several boat passages across the reef are situated on the NW side.

Underwater Morphology:

The underwater morphology is best shown by a bathymetric chart, which means depth information from the echo sounder graphs had to be plotted on a collector sheet. The extreme undulating bottom allowed only high and low points to be read off the graphs along each traverse.

A total of 8870 depths from 52 traverses, half highs and half lows were read off, corrected, reduced and plotted on an enlarged outline (scale 1:5,000) of the atoll. Final publication scale is 1:18,000. The volume of information on any one traverse made it impossible to show all the information in chart form. The great variability in depth of coral heads (highs) made the drawing of isobaths impossible. Consideration was given to showing the heads by symbol along each traverse, but their numbers precluded this. The lows, or areas between the coral heads, were contoured to show the bottom shape of the lagoon (Fig. 2), and this data is shown on the bathymetric chart of the atoll (Irwin & Main 1983).

Within the lagoon coral heads rise to the surface close to the SW shore but few do over the main body of the lagoon.

Echo sounder records showed the bottom to be covered with coral heads. Since they were evident on every sounding traverse, which gave good even coverage of the lagoon, the assumption can be made that this very high concentration of coral heads covers the lagoon floor. Figure 1 shows sample echo sounder records at selected positions across the lagoon. The Raytheon survey sounder used operated on a frequency of 200 kHz and has a transducer beam width of 10°. The high sounding rate on the scales used for the survey, 534 and 267 soundings per minute, with fast graph speed through the machine provided high resolution records. Simultaneous soundings using the Raytheon sounder with a Furuno model F850 sounder which has a lower sounding rate of 155 soundings per minute confirmed the Raytheon's superior resolution in these conditions.

The concentration of coral heads appear to be fairly uniform over the atoll basin to the deepest (30 + m) areas. Slightly higher concentrations of heads occur in the shallower areas, particularly the N end of Palmerston atoll. The height of the heads above the general atoll bottom is highly variable. The sounder did resolve small but definite flat sandy areas between the coral heads which were confirmed by first-hand observations and sampling by divers.

The inner edge of the reef is steep sided, the 5 m contour falling close to the inner reef edge. The 20 m contour also lies close to the inner reef edge except in the N sector which is shallower. The area within the 26 m contour, about 4 km x 3 km is comparatively flat, sloping to a low area 1.5 km x 1.2 km within the 30 m contour of similar shape to that of the atoll. This contains the deepest recorded depth of 34.6 m located to the S and E of the centre of the atoll. Isolated highs shown in comparatively deep water appear anomalous but these represent large coral head complexes which lie close to the sounding traverses.

Water Characteristics and Tidal Measurements:

Temperature and Salinity

Measurements were made at Palmerston Atoll on 11 September 1981 at 5 stations. Water temperature varied less than 0.5°C at any one

depth, at any sampling position, and less than 0.8°C from surface to bottom. Average surface temperature was 26.5°C decreasing to 26.2°C at 10 m, 25.8°C at 16 m, 25.7°C at 22 m and to the bottom at 30 m. Surface salinity was $35.47^{\circ}/\text{‰}$ increasing to $35.50^{\circ}/\text{‰}$ at 5 m, $35.54^{\circ}/\text{‰}$ at 10 m, $35.62^{\circ}/\text{‰}$ at 20 m and 35.66 at 25 m.

Tidal measurements

Measurements were made continuously from 4-17 September 1981 at Home Island inside the reef. Semi-diurnal tides recorded a maximum range of 0.51 m and a minimum range of 0.23 m over the period. The gauge on Primrose Island also inside the reef recorded a maximum range of 0.41 m and a minimum range of 0.25 m.

SUWARROW ATOLL

Suvarrow Atoll lies 950 kilometres NNW of Rarotonga. The atoll is near circular in shape with protrusions on the north and east sides, an entrance to the lagoon is located on the north-east side. Islands are situated around the reef except on the south west side. The lagoon is 15 km across E-W and 12 km N-S, the reef averages 0.5 km in width (Fig. 3).

Underwater Morphology:

The 10 sounding traverses run provide a sketch survey but the complex nature of the atoll with many reefs made drawing a bathymetric chart impractical. Figure 3 shows the atoll with sounding traverses, and selected sounder records are shown in Figure 4.

Suvarrow Atoll contains a number of reefs (up to 0.5 km long) which are exposed at low water. Coral patches and heads lie in shallow water areas close to the surface in the W, NW and E sectors inside the reef edge. Elsewhere deep water extends to the inner reef edge as shown by the soundings taken.

Many small coral heads are evident in the shallower areas. In the deep areas, the bottom exhibits highs with small coral heads on top, and relatively flat areas both with and without coral heads. Section 3-4 is a good example of these deeper flat areas. Samples of coral sand were dredged from clear areas.

Suvarrow Atoll with depths of over 60 metres is twice the depth of Palmerston Atoll. Soundings taken at Suvarrow reveal the bottom configuration to be quite different from Palmerston Atoll with a much lesser concentration of coral heads and relatively flat clear areas in the deeper parts (Figs. 1 and 4).

Water Characteristics and Tidal Measurements:

Temperature and Salinity

Measurements at 1 station on 21 September 1981 gave water temperature of 28.0°C at the surface and down to 24 m, decreasing to 27.9°C

at 32 m, to 27.8°C at 40 m and to 27.7°C from 40 m to the bottom at 64 m. Salinity over this depth ranged from 35.51-35.56 ‰.

Tidal measurements

Measurements were made using a tide gauge and semi-diurnal tides were recorded with a maximum range of 0.69 m and a minimum range of 0.51 m over a 48 hour period on 20-22 September 1981. Over a 14 day period a party on the island using a tide pole recorded readings from 9 to 92 cm, a range in excess of 0.80 m, but readings of peaks of high and lows may have been missed (C. Woodroffe pers. comm.).

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REFERENCES

- Hydrographic Chart Suvorov Islands 1922. 1:36,500, B.A. 1174.
- Irwin, J. & Main, W. deL. 1983. Palmerston Atoll Bathymetry 1:18,000, N. Z. Oceanographic Institute Chart, Miscellaneous Series No. 61.



Fig. 1. Palmerston Atoll, Echo Sounder traces DD¹, AA¹, BB¹, CC¹, refers to traverses marked in Fig. 2.

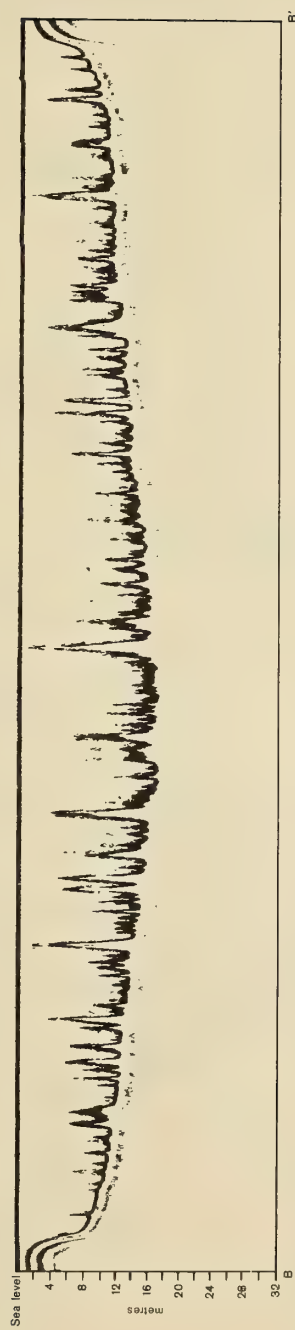


Fig. 1 cont'd.

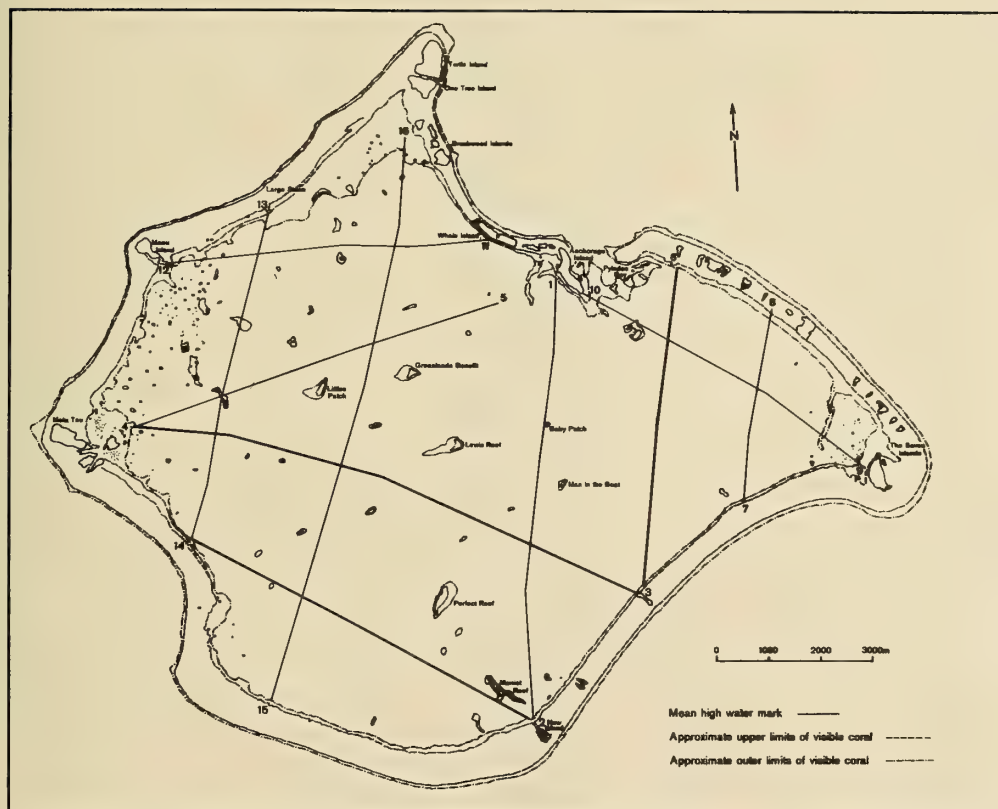


Fig. 3. Suvarrow Atoll showing echo sounding traverses. Heavy lines show traverses shown in Fig. 4. Track positions are approximate only.

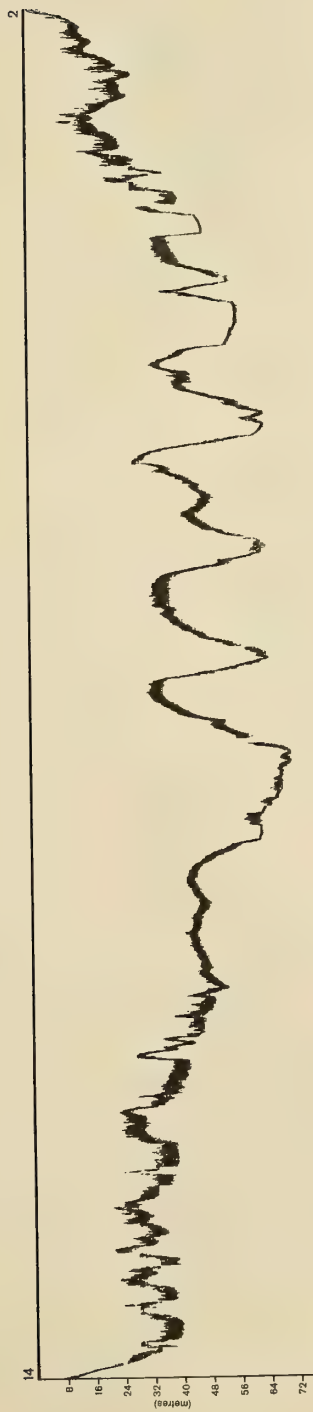


Fig. 4. Suvarrow Atoll Echo Sounder traces. 14-2, 6-3, and 3-4.



Fig. 4 cont'd.

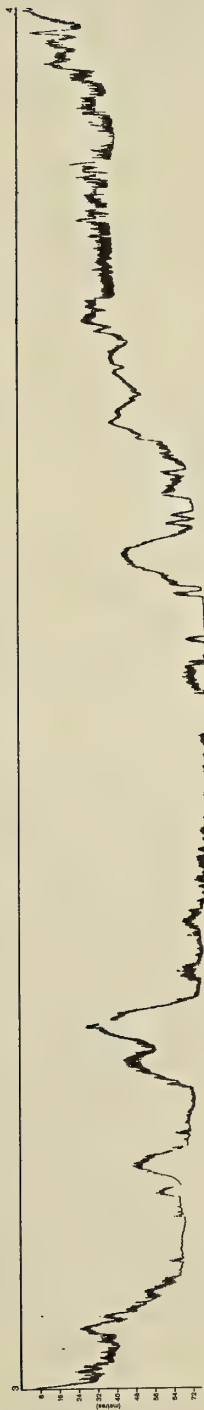


Fig. 4 cont'd.



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